3

Traditional oyster culture in France

Maurice Heral
IFREMER, Laboratoire National Ecosystemes Conchycoles (LEC), B.P. 133
17390 La Tremblade, France.

1 INTRODUCTION

The indigenous oyster of mainland France, the flat oyster, *Ostrea edulis*, has been part of the human diet for centuries. The Romans collected them and exported them to Rome. Although tanks for holding oysters after harvesting were in use at that time (Grelon 1978) it seems that true culture was not developed along the coast contrary to the records of Pliny the Older. It appears that oysters were already being captured on boards off the Italian coast. The exploitation of natural stocks continued through the Middle Ages and the Renaissance. However, it was not until the 17th century that oyster culture began, first in the pools of the salt marshes of the Atlantic coast and then in specially managed ponds. Papy (1941) repeats a good description given in 1688 of the oyster beds of the Marennes–Oléron which showed that stocks of flat oysters were by then being managed and improved. A decree by the Council of State in 1762 ordered the destruction of any oyster beds which prevented the circulation of water in the channels in the marshes. There is an article in the Encyclopaedia published in 1765 on the techniques of rearing in salt marshes which describes methods of culturing flat oysters from seed collected from rocks or dragged from natural beds. After two years the flat oysters were separated from each other and grown for four or five years' rearing in beds or 'claires'. Later, although other uses of the salt marshes declined for technical and economic reasons, oyster culture flourished (Lemonnier 1980). However, in the early days, the juvenile oysters all came from natural stocks.

From the 18th century natural beds on the Atlantic coast were overexploited, and from time to time decrees had to be issued forbidding the harvesting of flat oysters during the breeding season around the French coast (1750). Sometimes, as in the Arcachon Basin, interdicts totally forbidding the removal of oysters for several years were issued by the Admiralty. In 1755, the Parliament of Brittany issued an interdict forbidding fishing for 6 years in the Treguier beds. During the 19th century, in spite of increasingly strict regulations, stocks provided more and more variable returns. Fishing effort increased, stimulated by the beginnings of oyster culture with its high demand for seed brought in from the wild and by the increase in trade made possible by the improvements in communications (railways, postal system, etc.). Fishing effort on the Cancale oyster beds increased by 13 times from 1857 to 1872. Added to the effects of overfishing were the effects of variable recruitment in some years, as a result of extremely cold winters and the appearance of predators and competitors. Coste, in 1861, thought that the stocks from Cancale to Granville and those at Arcachon had been reduced, and those at La Rochelle, Charente, Oléron, and Marennes had disappeared. If modern oyster culture can be defined as the culture of oysters from captured spat it can be said to have begun in 1850. The developments of the techniques of spat capture were made by several different individuals. Since 1852, in the La Rochelle region, the spat of flat oyster has been captured on posts. From 1853–1859 De Bon and de Coste pioneered the use of wooden collectors similar to those in use in Italy. It was not until 1865 that Michelet developed the technique of liming tiles in the Arcachon Basin and the 'caisse ostreophile' which allowed the rearing of the young stages. From 1870, spat rearing-units were installed alongside oyster beds. From 1852, regulation of exploitations in the Domaine Public Maritime began, allowing coordinated developments to take place in estuarine regions.

From 1860, because of the shortage of flat oysters, cup oysters were imported from the mouth of the Tagus in Portugal to the Arcachon Basin. During one delivery, a boat, the *Morlaisien*, had to take refuge in the estuary of the Gironde. The cargo was ejected, and thus began the settlement of cup, or Portuguese, oysters (*Crassostrea angulata*) around the coast of France. This hardy species spread rapidly. In 1873 it covered the banks of the estuary of the Gironde (Verdon & Talmont). By 1874 it had reached the old flat oyster beds of the Marennes and Oléron regions and the Charentes estuary; by 1878, La Rochelle and the Ile de Ré and then the south coast of the Vendee. In 1923, a decree was issued forbidding the culture north of Vilaine because of problems caused when the new species, which had established itself throughout the south west, was grown together with the flat oyster, particularly around Arcachon. However, the Portuguese oyster could still be cultured in the Penerc and Etel rivers as well as in the Bay of Cancale. In the Marennes–Oléron area, settlement of cup oysters developed; the first samples in 1883 showed $\frac{2}{3}$ of the spat to be Portuguese and $\frac{1}{3}$ to be flat oyster. From 1923, capture became common in the mouth of the Charente and the Seudre on collectors made from strings of oysters, faggots, and stakes of hazel and chestnut. In 1910, the Portuguese oyster did not spawn in the Arcachon Basin, but in 1927, Hinard & Lambert stated that *C. angulata* had replaced *Ostrea edulis* on the collectors.

These developments in oyster culture were halted suddenly by massive mortalities which occurred among the flat oysters between 1920 and 1922 for reasons which were never fully understood but were probably caused by a disease brought on through unusual temperature conditions which either killed the adult oysters directly or upset their physiology because their diet was insufficient (Hinard & Lambert 1928). At this time the oyster farmers feared that the native oyster would disappear completely. However, settlement of *Ostrea edulis* began again fairly soon, in the summer of 1925 and then 1928. New, resistant populations appeared in South Brittany, particularly in the Auray, Crache, Po, and Plouharnel rivers. However, to the south of Vilaine Portuguese oysters have almost completely replaced the flat oysters.

First attempts at culture in the Mediterranean were carried out in floating parks off Sète. In 1900, suspended-culture methods began to be used in the étang de Thau; the oysters were attached to steel ropes with cement. At the same time, at Seyne and at Marseille, rearing operations began on the sea bed in shallow waters (3–4 m) with several million flat oysters being produced in the étang de Thau. In 1932, the only oyster culture present in the étang de Thau was in one concession between Bouzigues and Mèze. From that time, oysters purchased in Brittany were stuck onto posts individually with cement. These were suspended from a framework in the mussel parks. Mediterranean, oyster culture has developed only recently. The flat oyster was cultivated in suspension in the Mediterranean up to 1950–51, years during which the stock was severely reduced. Stocks were then replaced with Portuguese oysters.

On the Atlantic coast, intensive oyster culture developed up to 1960 (85 000 tonnes of *C. angulata*, 28 000 tonnes of *O. edulis*) (Fig. 1). During the development of production, rearing became concentrated in favoured sites, more or less enclosed by bays where they are protected from the worst of the weather. In the largest rearing basins (Marennes-Oléron, Arcachon, etc.) the growth of oysters decreased and mortalities increased. An increasingly large percentage appeared to 'stagnate'; oyster farmers described them as being 'sulky'. From 1966 to 1969, in different French oyster-producing regions, Portuguese oysters suffered from gill disease. Massive mortalities between 1970 and 1973 caused the disappearance of the Portuguese oyster from the French coast.

The import of the Pacific oyster, *C. gigas*, began a new phase of oyster production from 1972 onwards. However, in 1975, a drop in yield from the stocks occurred again, at the same time as numbers were being increased. This happened particularly in the Marennes–Oléron region, Arcachon, and the Bay of Bourgneuf. During this same period, the flat oyster, *Ostrea edulis*, was attacked successively by two parasitic diseases; *Marteila refringens* from 1974 and *Bonamia ostreae* from 1979. The parasites occurred in almost all the centres of flat oyster culture (Fig. 1).

In 1984, the production of oysters in France (100 000 tonnes) was made up of 98% Pacific oyster, cultivated over an area of 20 000 ha.

This brief history demonstrates how, over a century, several features have recurred in the French oyster industry. There have been successive phases of over-exploitation of natural stocks of the flat oyster, diseases, the importation of a foreign species (*Crassostrea angulata*), high density culture, and diseases again (of flat and cup oysters) leading to the need for new imports (*C. gigas*). This points to the need to manage the culture beds toward an ecological and physiological equilibrium for the species so that the oyster stocks are better able to withstand attacks from pathogens.

2 ASPECTS OF THE BIOLOGY

2.1 Classification and geographical distribution

Using the criteria given by Grasse (1960), oysters belong to the molluscs, Class

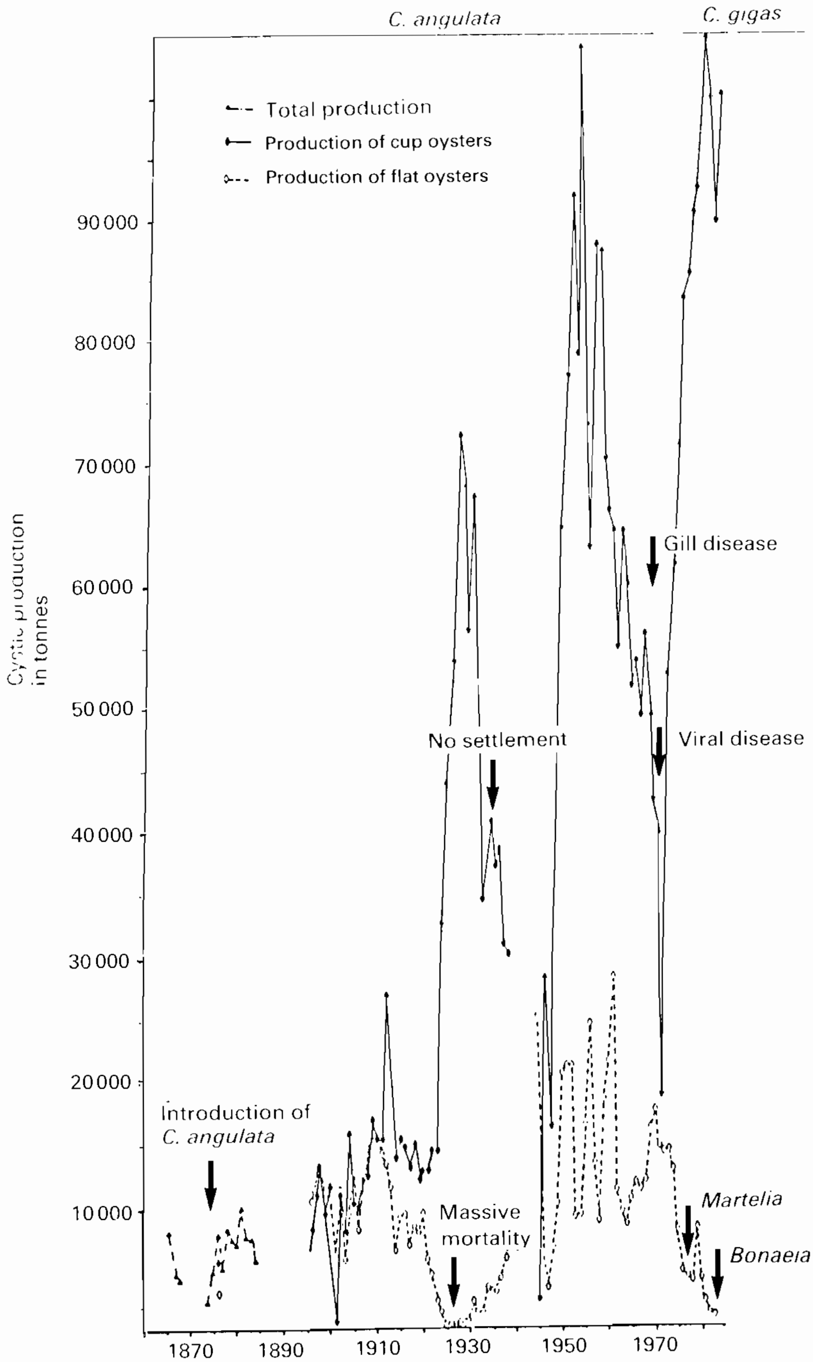


Fig. 1 — Changes in oyster production in France from 1865 to 1983 (statistics form Marine Marchande; after Héral 1986).

bivalves or lamellibranchs, Order Filibranchs and the Family Ostreidae, with two genera cultivated in France: (Fig. 2):

☐ Genus *Crassostrea* Sacco 1897

Represented by two species of cup oysters; *Crassostrea angulata* ⓛ the Portuguese oyster and *Crassostrea gigas* Thunberg, the Pacific oyster. In the adult oyster the shell is elongated and ridged, the left shell is domed allowing the visceral mass to develop, while the right shell is flat and, for the Pacific oyster, marked by a series of 'curls'. These oviparous oysters, which have a high fecundity, live in the intertidal zone. They have a high tolerance of low salinities and can thus spread into estuaries.

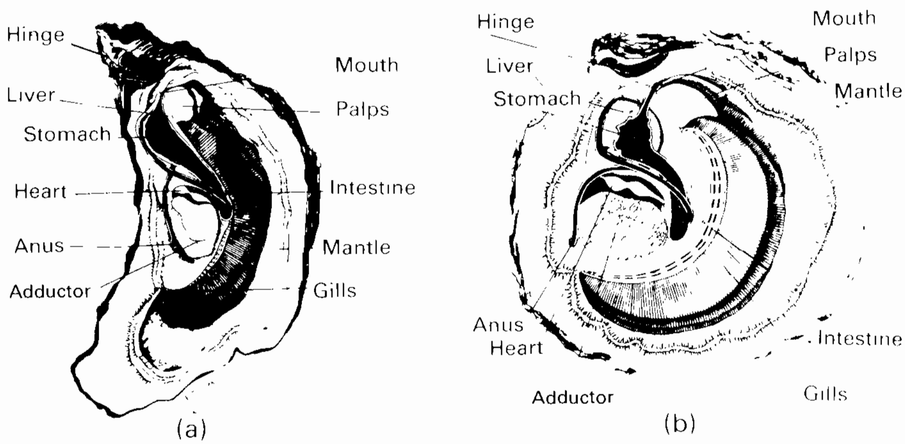


Fig. 2 — Anatomy of the two species of oyster cultivated in France. (a) *Crassostoea gigas* (cup or cupped oyster); (b) *Ostrea edulis* (flat oyster).

C. gigas is a native of the Pacific ocean, being found in the Sea of Okhotsk (Vladivostok), Sakhalin (USSR), in Japan where there are two local races in the Iwate and Hiroshima prefectures, in Korea, and along the Pacific coast of North America from Alaska through British Columbia and then through the United States to California. It was brought to France in 1966 when there was a large-scale import of seed from Japan (Sendai and Hiroshima). In 1972 there were imports from British Columbia to build up the naturally reproducing stocks.

Some experts believe that *C. gigas* and *C. angulata* are the same species. Ranson (1951, 1967) found identical larval characteristics. Menzel (1974) obtained viable hybrids by crossing the two types of oyster. Buroker *et al.* (1979) studied the genetic variation of proteins and enzymes and found a similarity of 99% between the two forms for 24 loci studied. They put forward the hypothesis that Japanese oysters may have been transported to Portugal on boats which were making frequent voyages in the 16th and 17th centuries. However, the oysters do show some different characteristics: respiration rate, filtration rate, growth, type of reproduction, and different susceptibility to diseases, suggesting two races with distinctly different physiologies.

☐ Genus *Ostrea* Linnaeus 1758

Represented by *Ostrea edulis*. The adult oyster has a roughly circular shell. This species is viviparous and has a lower fecundity. It is more of an oceanic mollusc than the cupped oyster, preferring water of relatively high salinity and low turbidity. Natural and cultured beds are found below the low tide mark or in areas always covered by water. It is a native of northern Europe, from Norway to France, through Denmark, Germany, the Netherlands, Belgium, Great Britain, and Ireland. To the south it is found on the Atlantic coast through Spain, to as far as the south of Morocco. In the Mediterranean it is found in France, Italy, Sicily, and also Morocco and Tunisia. Its distribution extends to the Adriatic and Black Seas.

2.2 Physiology

Lucas (1976) reviewed the literature published since the start of the 20th century on reproduction, the detection of larvae, ecology of the culture-bed ecosystems, and population dynamics of the molluscs, showing that these had been well understood, as had the control of disease and the health of the oysters. This had allowed the development of modern aquaculture and the planning of its day-to-day operations.

Specialist works covering the life cycle of the oyster include the *Traité de Zoology* (Grassé 1960) and the *Manuel de la conchyculture* (Vols 1,2,3, 1974, 1976, 1979). In this section, the most recent biological information necessary to understand the rearing procedures is detailed.

2.2.1 Nutrition

The oyster has two ways of absorbing food: either directly absorbing dissolved substances present in the sea water or through the ingestion of particles in suspension (Fig. 3).

☐ Direct absorption of dissolved organic matter (DOM)

Experiments carried out by Ehrnard & Heinemann (1975), Fevrier (1976), and Fankboner & De Burgh (1978) indicated that lipids in solution in sea water can be absorbed rapidly by the molluscs.

Sorokin & Wyshkwarzev (1973), Pequinat (1973), Bamford & Gingles (1974), Wright & Stephens (1978), Elliott (1979), Amouroux (1982), and Jorgensen (1982, 1983), established the kinetics of the absorption of amino acids and glucose in the gills and the mantle where digestive activity is extremely intense. Recent work, using high-resolution chromatography with whole animals, has demonstrated the active absorption of amino acids. These results can be added to those on nutrition on artificial diets based on sugars and oils carried out by Castel & Trider (1974).

Empirical observations made by oyster farmers have shown that the inflow of fresh water from the rivers leads to increased growth in oysters, which cannot be related entirely to the fact that salinities are low. The direct absorption of organic matter may involve the intake of substances which act as growth factors. Collier *et al.* (1953) demonstrated the extremely beneficial effects of carbohydrate present in the marine environment to the filtration rate and internal activity of molluscs. Recently, Heral *et al.* (1984) put forward evidence to show that the concentration of dissolved

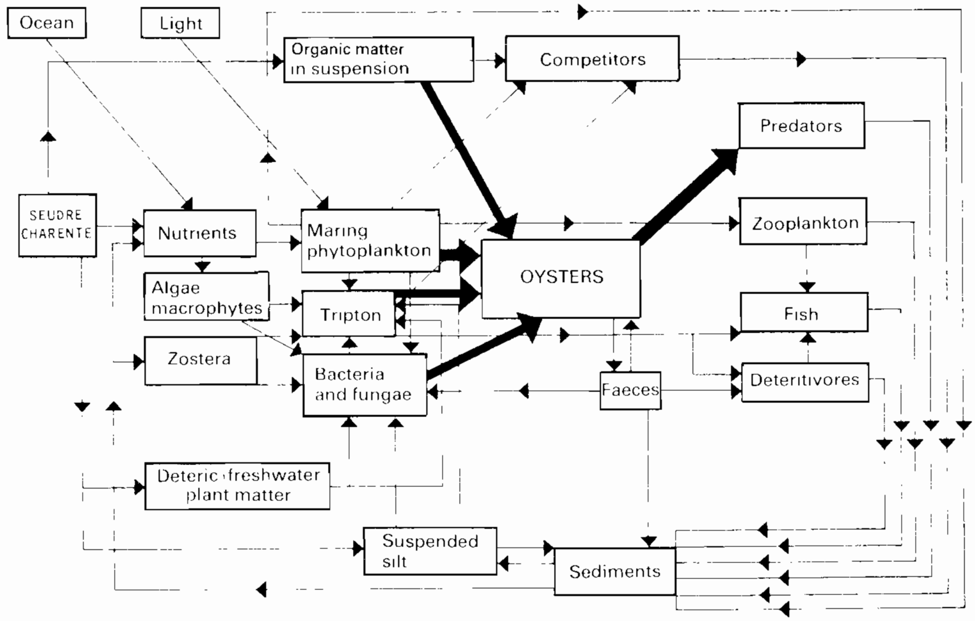


Fig. 3 — Ecosystem of an oyster bed in the Marennes–Oléron Basin (after Héral 1977).

organic carbon and nitrogen compounds in the Marennes–Oléron region was highly correlated with the production of flesh in oysters of between 1 and 2 years of age. This absorption was equivalent to 5% of the particulate energy actually absorbed (Heral *et al.* 1987).

□ Ingestion of suspended particles.

Mineral and organic particles are filtered and retained on the surface of the gills and surrounded by mucus. They are then directed towards the labial palps by rows of cilia on the gills. It is likely that these cilia and the labial palps carry out effective qualitative grading of the food, thus effectively enriching the diet at the beginning of the digestive process. The food is then ingested and partly digested in the stomach which contains the crystalline style and digestive enzymes (amylase, glycogenase, cellulase). Digestive diverticulae also have an intracellular digestive function (Wilson & LaTouche 1978) in *Ostrea edulis*. The remainder passes through the intestine and is evacuated through the anus as faeces. When particulate matter is too abundant or too large it is ejected by the gills and labial palps or bound together by mucus, dropped into the mantle, and ejected in the form of pseudofaeces.

The rate of particle retention or the filtration rate is defined as the quantity of water thoroughly 'purified' by the molluscs and is expressed per hour per gram dry weight of mollusc flesh (gdw). Most authorities calculate this by using an indirect method in closed containers where the consumption of phytoplanktonic algae can be monitored for a fixed period. It varies principally with temperature, quantity and quality of food, current, and the size of the mollusc (Widdows 1978).

It appears that, at the same temperature, the Pacific oyster filters at five times the rate of the flat oyster (Table 1). *C. gigas* seems to possess a mechanism whereby

Table 1 — Rate of retention of particles for the cupped oyster and for the flat oyster

Authors	Fiala-Médioni & Copello (1984)	Gerdes (1983)	Deslous-Paoli *et al.* (1987)	Rodhouse (1978)
Species	*C. gigas* adult	*C. gigas* adult	*C. gigas* adult	*O. edulis*
Temperature	15°C	20°C	4°–25°C	5 à 20°C
Phytoplankton species	*Phoeodactylum tricornutum*	*Isochrysis galbana*	Natural food	*Tetraselmis*
Size	3 à 9μ	3.5 à 4μ	1 à 25μ	—
Rate of retention or filtration in $l.h^{-1}.gps^{-1}$	2.1 with 27.5×10^6 cell.l^{-1}	3.8 with 100×10^6 cell.l^{-1}		0.4 à 5°C
	5.8 with 10.5×10^6 cell.l^{-1}	4.7 with	3 à 9.5	1.4 à 15°C
	12.3 with $0,1\times10^6$ cell.l^{-1}	5.8 with 50×10^6 cell.l^{-1}		2 à 20°C

filtration is regulated in relation to the number of phytoplanktonic cells. With natural food (organic/mineral mixture), filtration efficiency is optimal between 6 and 10 μm particle size. When the density of particles is greater, filtration efficiency is higher with the small sized particles (Fig. 4). Elsewhere it was found that at 5°C, retention

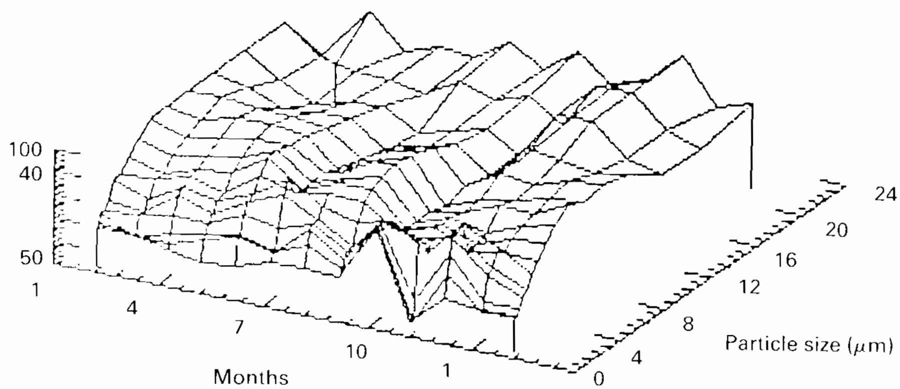


Fig. 4 — Annual cycle in the efficiency of retention of the oyster (*Crassostrea gigas*) in relation to the size of the particle characteristic of the estuarine environment (after Deslous-Paoli *et al.* 1987).

reached 10 l/h/gdw while at the same temperature the flat oyster is almost inactive (Table 1). The difference in activity between the flat oyster and the Pacific oyster results in a different pattern of food consumption which has consequences for both the growth and the fattening of the two species.

2.2.2 Reproduction

Adult oysters reproduce sexually. Spawners produce male or female gametes. The species *Ostrea edulis* changes sex, producing male or female gametes successively but not at the same time. Marteil (1976) showed that the flat oyster is male in the autumn following settlement. The spermatogonia break down and the ovaries develop in the following season when the oyster will be a female. *C. gigas* differs from this; the oyster can function as a male or as a female during one season before changing sex during the following year. Some hermaphrodite individuals persist. The environment (temperature and nutrition) and also internal hormonal factors apparently control the determination of the change of sex.

☐ Effect of temperature on gametogenesis

For *C. gigas*, correlations between the date of spawning and the cumulative monthly temperatures measured from 1972 to 1985 in the Marennes–Oléron Basin provide evidence of significant inverse correlation between the temperature in the autumn preceding spawning and the date of spawning (Heral *et al.* 1986). Lubet (1980) showed the importance of autumn temperatures on the early stages of gametogenesis. However, there appears to be no connection with winter temperatures and, finally, the effect on the speed of gametogenesis. The degree-day sum from September to June gave a provisional equation for the date of spawning (y) but when temperature (T) falls below 15°C the gametogenesis of *C. gigas* is significantly retarded, speeding up again when temperatures increase (Mann 1979).

$$y = 282 - 2.87\,(T,\ \text{September to February}) + 1.078\,(T,\ \text{March to June})$$
$$R = 0.9227$$

The comparative study of reproduction in two years (1979 and 1981) gives evidence of the supplementary indirect effect of temperature, through the food chain, on gametogenesis. There appears to have been a significant deficit in assimilable particulate organic matter, both phytoplanktonic and detritic, for all of the beginning of 1981 compared with 1979. The food deficit, linked with lower temperatures, caused a significant depletion in glycogen and lipids in males and females (Fig. 5), resulting in a low, or even absent recruitment in 1981, while in 1979, a single massive spawning in August resulted in strong recruitment (Deslous-Paoli 1981).

Marteil (1976) found that the minimum temperature for the start of gametogenesis for *Ostrea edulis* was 10°C, and that for spawning between 14 and 16°C. Unlike *Crassostrea gigas*, *Ostrea edulis*, when kept in a hatchery, has a period of sexual dormancy (Lubet 1980) which is likely to occur in December. Other workers have demonstrated the importance of the nutrition of the spawners. Helm *et al.* (1973) showed experimentally that giving supplementary nutrition during gametogenesis leads to more rapid larval growth.

☐ Number of broodstock required

There are two possibilities: either the stock is very large, sometimes too large, and

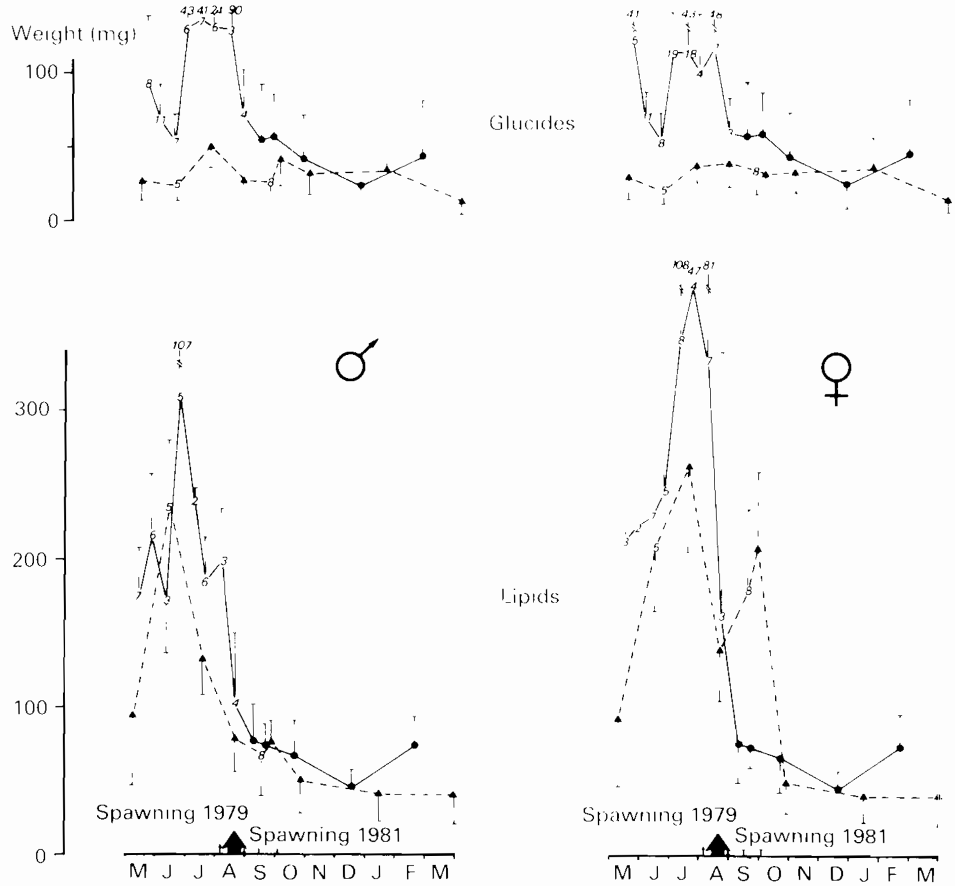


Fig. 5 — Change in glucide and lipid composition for standard 50 g male and female oysters during 1979 (●) and 1981 (▲) (after Deslous-Paoli *et al.* 1982).

the relationship between stock and recruitment will be through the food web, or the stock is very low and reproduction becomes chancy. In this latter case it is necessary to determine the minimum stock level necessary to maintain recruitment. In Marennes–Oléron, at the time of disappearance of *Crassostrea angulata* and its replacement by *C. gigas* in 1972, while the stock of *C. angulata* dropped to 15 000 tonnes and while there were no more than 8 000 tonnes of *C. gigas*, no further recruitment took place. However, the same numbers of larvae as in the preceding and succeeding years were found in the water, but these larvae did not develop and settle. It appears that, in spite of the critical state of the stock at this time (viral disease and gill disease, Comps (1970), Comps *et al.* (1976)) it was not the level of the stocks but other factors acting on the larvae which prevented recruitment. However, the problem became more crucial for *Ostrea edulis* when the stock was seriously depleted by different parasites.

☐ Age structure of the population.

The cultivation of stocks by man has entailed the regular removal of the oldest animals. These removals free part of the biotic capacity of the environment and allow a more rapid rotation of stocks with a consequent increase in production and rejuvenation of the cultivated population. While this 'rejuvenation' appears to increase the quality of the gametes and therefore the larvae, it brings a decrease in the mean fecundity of the population.

While a three-year-old cupped oyster produces around 80% of its body weight in gametes, a two-year-old oyster produces no more than 60%, and a one-year-old only 7% (Deslous-Paoli & Heral unpublished). For *C. gigas*, where the mean individual fecundity is several tens of millions of oocytes, the lowering of the population age may be compensated for by the sheer volume of the stock in culture. However, for *Ostrea edulis*, where the mean fecundity is between 500 000 and 1 million eggs and where stocks have decreased drastically, a significant lowering of average age can have consequences for recruitment.

☐ Spawning and larval life

When the gonads are mature, the spawners expel the gametes. In the flat oyster, fertilization takes place in the pallial cavity with spermatozoa brought in on the water current. The larvae are incubated there for 8–10 days before being liberated into the external environment. They are slate-grey in colour.

For the cupped oyster, fertilization takes place in the sea at the mercy of the currents and by chance meeting of the sperm ova. Trochophore larvae develop and rapidly produce a two-valved shell. The D-shaped veliger larva, at 24 h measure 70 μm for *C. gigas* and 160–200 μm for *O. edulis*. The shape of the larva changes as it grows. After around 10 days (150 μm for *C. gigas* and 200 μm for *O. edulis*) a sort of hook, the umbo, develops. Several days later, at a size of 290 μm, a foot develops which allows the 'pediveliger' to move round by using its velum and to seek out a suitable substrate for attachment with the byssus. The byssogenic gland rapidly secretes cement which sticks the oyster to the substrate. Metamorphosis occurs next; the foot and the velum disappear and the resulting larva is termed the spat. For *C. gigas*, larval survival appears to relate more to temperature than to salinity. Analysis of the temperature–salinity chart over the period of larval development in the Marennes–Oléron Basin, in 1980–1986, shows that at a temperature below 17°C there is a deficiency of recruitment, as happened in 1981 and 1986 (Fig. 6).

The length of the larval stage depends mainly on temperature. For *C. gigas* it varies between 15 and 28 hours. The survival rate *in situ* may reach 10% in the years when larval development takes place satisfactorily (Fig. 7). For *Ostrea edulis*, the planktonic phase is 8–14 days, depending on temperature (Marteil 1976) and the survival rate may reach 10% at 22°C. However, not all emissions result in settlement, and it is essential that temperatures should be above 15–16°C.

The action of salinity seem less important. In Japan, *C. gigas* survives and reproduces over a range of salinities; but there seems to be a correlation between the temperature and salinity for successful reproduction. However, even though *C. angulata* does not reproduce in the Mediterranean and the same appeared to be true for *C. gigas* after its introduction, it now appears to reproduce in Yugoslavia and occasionally in the étang de Thau even though the salinity has not varied.

The optimum salinity was determined to be 25‰ by Helm & Millican (1977),

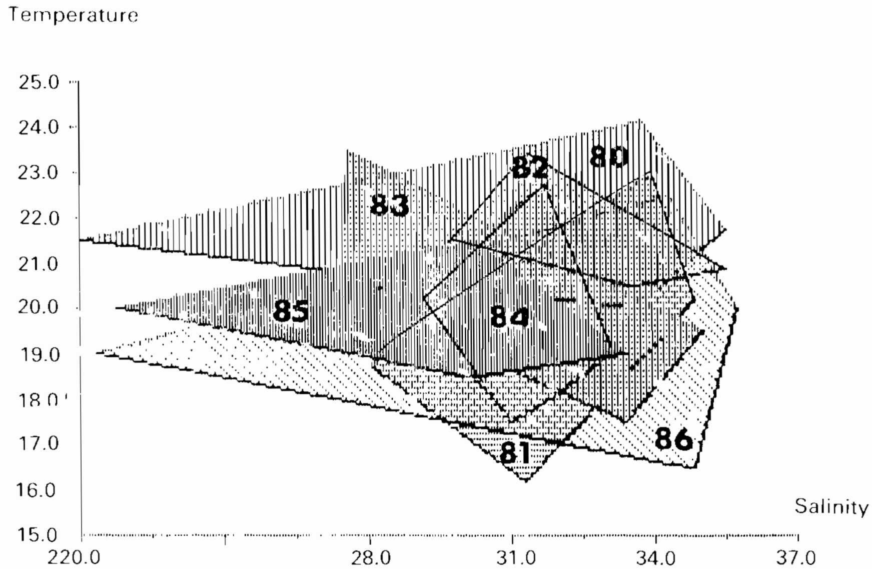


Fig. 6 — Temperature and salinity during the period of larval development for the oyster (*Crassostrea gigas*) in the Marennes–Oléron Basin (after Prou & Héral, unpublished).

and was verified experimentally at Arcachon. Nevertheless, it appears that the tolerance of *C. gigas* allows good recruitment even at 20°/₀₀, as in the Gironde. This species appears to be relatively independent of salinity, as is shown by studies on the influence of salinity in the Charente estuary on the settlement in the Marennes-Oléron Basin for *C. gigas*.

Although the problems of larval nutrition can be dealt with in a hatchery, they are not well understood in the wild (Lucas 1982). Experimentally, growth of *C. gigas* larvae is better when mixtures of algae are used rather than monospecies cultures (Millican & Helm 1983). Despite this, the size of the particles used by wild oysters remains to be determined, as does their composition. Although it has been shown that bacteria are used as food by larval bivalves (Martin & Mengus 1977, Prieur 1980), the part they play in nutrition has been ignored. It has been shown that larvae can use dissolved organic substances (Stephens & Manahan 1983), but it has not yet been determined whether these are a source of energy or whether they have a role as growth factors. On the one hand, in the Arcachon region it appears that the disappearance of nanoplankton (His *et al.* 1983) brought on by human-related factors was largely responsible for the absence of recruitment from 1977 to 1981. Conversely, the work of Miller and Scott (1967) showed that *O. edulis* larvae can fast for 3–4 days and then resume normal nutrition when food is again available.

To make short-term predictions of the date to install collectors and to inform oyster farmers, the different IFREMER laboratories (La Trinité, La Tremblade, Arcachon, La Rochelle) carry out bi-weekly surveys of the abundance of larval oysters present in sea water. After the spawning of oysters has been detected, the

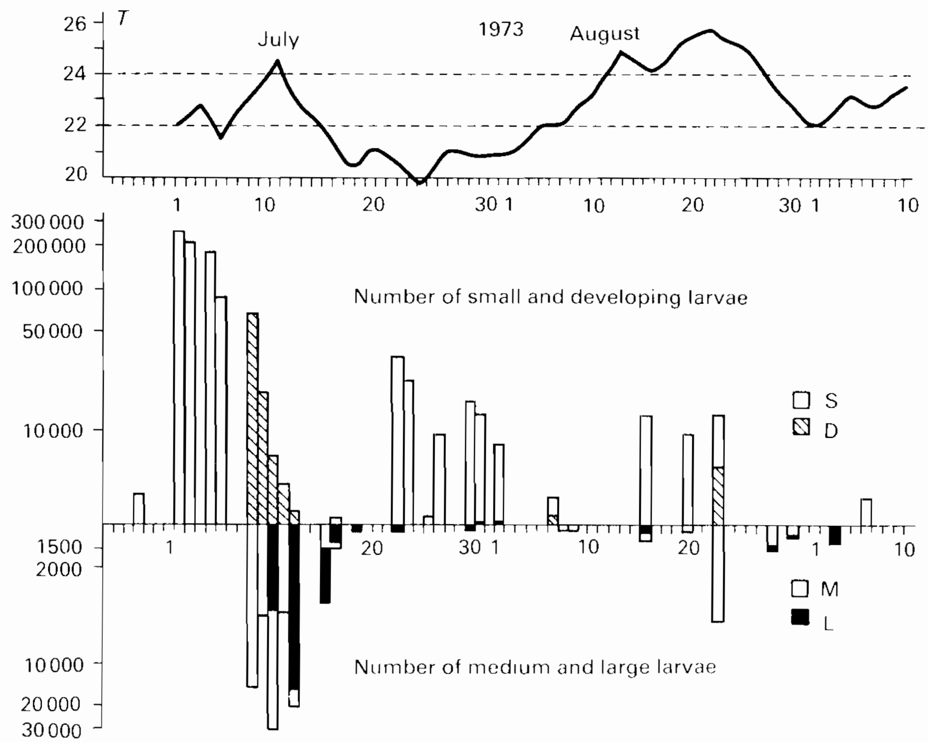


Fig. 7 — Change in the number of small (S) and developing (D) medium-sized (M) and large (L) larvae for *Crassostrea gigas* at Arcachon (after His).

veliger larvae of *C. angulata* in the past, and *C. gigas* and *O. edulis* now, are monitored up to the attachment stage.

A chronological sequence of the abundance of larvae ready to attach shows up years where there is an absence of settlement, and this can be checked against information in the public archives (Fig. 8).

In the Marennes–Oléron, the series of the abundance of larval oysters from 1925 to 1972 for *C. angulata* and from 1972 to 1986 for *C. gigas* shows an absence of recruitment for *C. angulata* in 4 years out of the 47 where data are available, and for *C. gigas* an absence of recruitment in 3 of the 11 years available. In the Marennes–Oléron Basin the capture of *C. gigas* is more uncertain than that of *C. angulata*; this appears to be due to the higher temperature requirement for the Pacific oyster for the maturation of spawners and the survival of larvae.

By contrast, in the Arcachon region during those same 11 years, spat settlement failed in 7 years because the area is subject to man-made disturbances which have a profound influence on the mechanism of the development of the larval oysters.

☐ Action of man-made influences

There was no recruitment of oysters in the Arcachon Basin between 1977 and 1981.

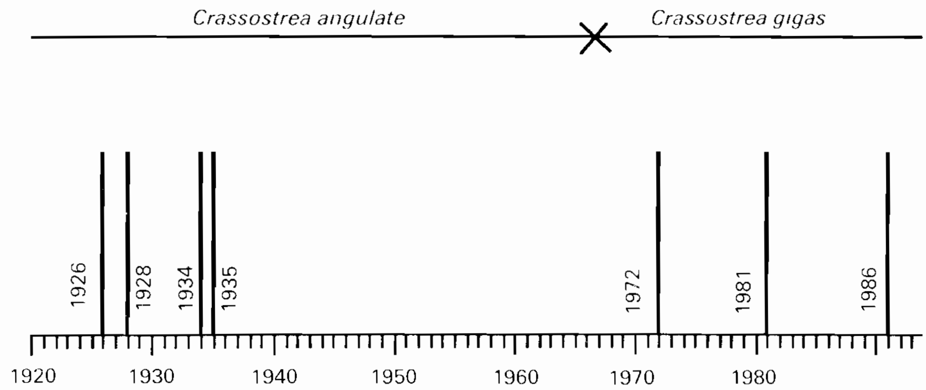


Fig. 8 — Years of zero spat capture (|) for *Crassostrea angulata* and *Crassostrea gigas* in the Marennes–Oléron basin.

This was caused by perturbations in the progress of development of the pelagic larvae of *C. gigas* during the first days of their lives. Pigmentation of the veligers was reduced and growth ceased, so that the larvae did not reach the stage where the foot begins to develop. The veligers do not show any abnormalities in their developing shells, and there appears to be no relationship between failure and temperature. Three hypotheses have been put forward to explain this phenomenon: defective gametogenesis in the spawners in the Arcachon Basin, mortality of the larvae caused by the direct action of pollutants in the water in that area, or a change in the food supply to the veligers. Observations and experiments have been carried out on the veligers obtained from controlled environments or veligers collected from the wild and put into a controlled environment, and on the algal food supplied to the veligers in the controlled environment. Results showed that the quality of the spawners and the 'biological quality' of the water in the Arcachon Basin were sufficient to allow the development of the veligers (Robert 1983). This suggests that the failures in larval development may be related to food. Amongst others the use of anti-fouling paints based on organometallic compounds has been shown to affect not just embryogenesis and larval development in *C. gigas* (His & Robert 1980, Robert & His 1981) but also the growth and cell division of *Chaetoceros calcitrans* and *Isochrysis galbana* (His & Robert 1981). Measures forbidding the use of organo-tin anti-fouling paints have been effected, and they coincided with a return of spat settlement from the summer of 1982 (His *et al.* 1983).

2.3 Energetics

In species cultivated at high density in controlled or semi-enclosed environments, it appears that factors such as the limited quantity of available food and the ability of the organism to use this food have a strong influence on production. Thus for sessile molluscs cultivated at a high density in a confined environment it is necessary, at the same time as determining models of overall production, to determine the different forms of nutrient available and also the dietary requirements not only of the cultivated molluscs but also of non-cultivated species in the locality.

This energetic concept holds the key to the analysis as it encompasses a wide range of mechanisms under a single unifying concept, as described by Odum (1971).

Many laboratory studies (Walne 1970, Thompson & Bayne 1974, Widdows 1978) have shown that growth in bivalves is directly related to the amount of food supplied to them. Few of the studies have covered both the food present in the environment and the feeding behaviour of the molluscs living there. Bernard (1974) for *C. gigas*, Widdows *et al.* (1979) for *Mytilus edulis*, and Vahl (1981) for *Chlamys islandica* have shown, at various levels, that organic matter is the main source of food, and have thus been able to establish the energy budgets and nutrition of these species in relation to particular environmental conditions. Other studies, using small-scale laboratory experiments (Winter 1976, Widdows *et al.* 1979, Griffiths 1980, Kiorboe *et al.* 1981) have shown differences between cultures in water containing phytoplankton alone and those with a mixture of algae and minerals. These mixtures resemble conditions found in estuaries, and they demonstrate that the influence of minerals and detritus in suspension on the assimilation of molluscs is, in effect, to dilute the food.

Little information on the abundance of potential food in areas where molluscs are reared intensively is available in the literature. In practice, the complete range of nutrients of different origin is not taken into account, although some excellent studies have concentrated on one small aspect, ignoring the others. It is thus difficult to review the whole system (Heral 1987).

Looking at the relationship between oysters *in situ* and the environment, Deslous-Paoli *et al.* (1981) showed that there was a light relationship between the biochemical constituents of *C. gigas* and the richness of the organic content of the water, principally the phytoplankton. The same workers (Deslous-Paoli *et al.* 1982) put forward the theory that, when there is a shortfall in the quantity of nutrients available, the products of the gonads fail to develop and mature satisfactorily.

Energy equations and indices of conversion differ between authors. The definitions used here are those given by Lucas (1982). The general equation for the energy budget of a population of oysters can be written as:

$$A=P+R=C-(F+U)$$

Where A = assimilation
P = production
R = respiration
U = excretion of soluble substances
C = food consumed

Production is composed of:

$$P=Pg+Pr+Ps$$

Where Pg = production of organic matter in the tissues
Pr = gamete production
Ps = production of the organic matter of the shell and mucus secreted.

Assimilation efficiency (A/C) and crude production (P/C) are calculated by the method given by MacFadyen (1966).

Production, *Pg* is the quantity of energy accumulated in the tissues during growth; Fig. 9 shows the increase in dry weight of a population of *C. gigas* over 3 years. *Pg* can

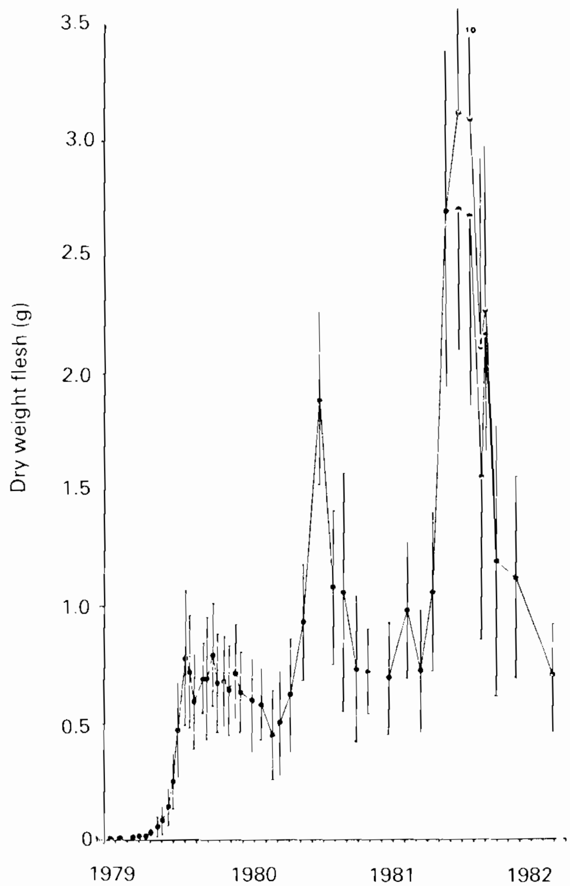


Fig. 9 — Change in dry weight of flesh of *Crassostrea gigas* caught in 1978. Vertical bars: variance, females, males (after Deslous-Paoli & Héral 1987).

be determined from micro-bomb-calorimetry as can the quantity of energy necessary for the production of the shell (Fig. 10).

Pr, production of gametes, is estimated indirectly by finding the difference in the energy content of the oyster at the stage of maximum gonad development and after completion of spawning.

Respiration, *R*, is the active metabolism of the mollusc, i.e. the energy necessary

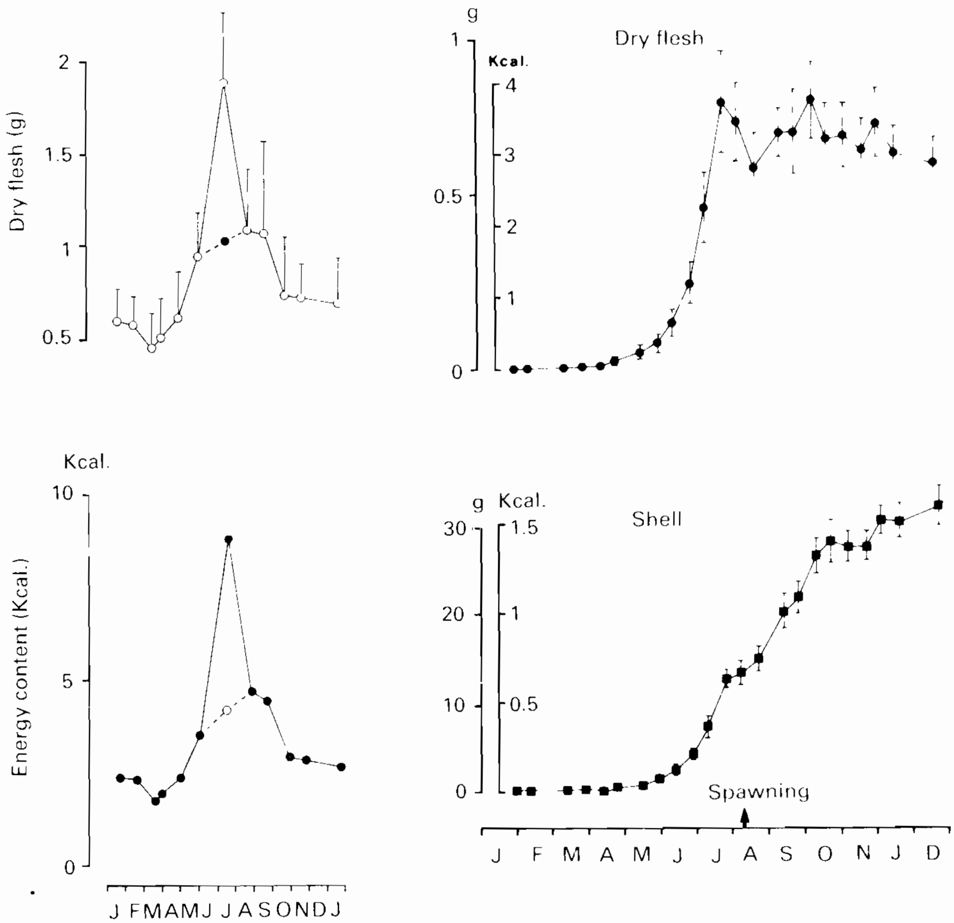


Fig. 10 — Monthly variations in the mean energy value of dry flesh (Pg) of one-year-old oysters (1), and two-year-olds (2), shell of three-year-old oysters (3) and four-year olds (4) (after Herál *et al.* 1983 Deslous-Paoli & Héral 1984).

for all the chemical reactions which keep the animal alive. Bernard (1974) studied respiration in relation to water temperature in *C. gigas*. Results were low compared with those of Boukabous (1983), Copello (1982), Gerdes (1983), and Heral *et al.* (1987).

Faeces and pseudofaeces (*F*) is the quantity of biological wastes excreted by the molluscs determined *in situ*, using traps arranged around the culture beds. The technique used in the intertidal beds is given by Sornin (1981). Estimates of their energy content are made by the same methods as those used to estimate the energy content of organic matter in water.

Urine excretion (*U*), is generally not measured; the only figures are for nitrogen excreted by *C. gigas* (Mann 1979, Griffiths 1980). However, excretion of organic forms of nitrogen by *C. gigas* is far from negligible. Results, although incomplete (Robert *et al.* 1981), show that in the summer months 77–93% of nitrogenous waste is in the organic form. Heral *et al.* (1987) measured urea excretion in *C. gigas* which was found to be low (0.25 μmole/h/g dry weight), while excretion of amino acids can reach 2 μmole/h/g dry weight in summer.

A study of the energy budget, carried out in the Marennes–Oléron Basin, the foremost European oyster culture region, showed that production for young oysters is highest in June and July and negative in the autumn. In older oysters, the two periods of negative production, one in winter and one in summer after reproduction, give gross and net yields which are largely negative. Shafee & Lucas (1982) found two periods of negative production for the scallop *Chlamys variae*. For *C. gigas* cultured in the Marennes–Oléron Basin it appears that there is a particularly long period of negative production (around 6 months) which causes a progressive wasting of the oyster as reserves are consumed.

The other characteristic of this estuarine region is the high rate of deposition of organic matter throughout the year, but particularly in the winter. This is linked to the high levels of seston in the water (Sornin *et al.* 1983). The energy from this accounts for 73.8% of the energy consumed by the young oysters. This gives mean annual assimilation rates of 26.2% for juveniles and only 7.9% for adults. The yields are much lower than those given in the literature for other species. Bernard (1974) showed that large quantities of organic matter were not assimilated, but rejected either directly by the labial palps as pseudofaeces or remain undigested during their passage through the gut, suggesting that *C. gigas* is either inefficient or highly selective qualitatively in its digestive capacity or not adapted to life in the extremely turbid water which clogs the gills and has a negative effect on assimilation.

In practice, the high turbidity in winter linked with a low level of organic matter induces a high production of pseudofaeces and, correspondingly, an expenditure of energy in sorting the particles, mucus secretion, and branchial cleansing. This explains the poor performance of adult oysters in the Marennes–Oléron Basin. However, after reproduction which is an important part of the energy balance (84% of production of adult oysters), the negative yields in September and October may come from a lack of food, particularly phytoplankton; the mollusc may not have sufficient usable energy available. This autumnal deficit varies from year to year; it depends on the quantity of phytoplankton as well as the density of consumers which include other molluscs in culture and wild competitors.

☐ Transfer of energy between the water column and the mollusc population

At the same time the quantity of energy from the particulate food has been studied every month in relation to time and the tidal coefficient. Taking the currents into account, this allows the establishment of the mean monthly quantities of energy available (Heral *et al.* 1983, Deslous-Paoli & Heral 1984).

Thus it can be seen that in the same region (Marennes–Oléron) the quality of the food available is controlled by the huge input of detritus. The potential food available for the molluscs was given by Widdows *et al.* (1974) in terms of the sum of proteins, lipids, and glycogen, and represented only 2.6% of the total seston and 24.385 of the organic matter, on average. However, phytoplankton appear to play a major role with the periods of development corresponding to high production of the oyster. The heterotrophic bacteria appear to be only a nutritional complement as they represent a mean of only 0.6% of the total energy.

Examination of the quantity of food which passes through the 10 cm of water around the banks of oysters shows that the transfer of energy with the surface water appears to be very low, around 1% (Figs 11, 12). This does not take into account

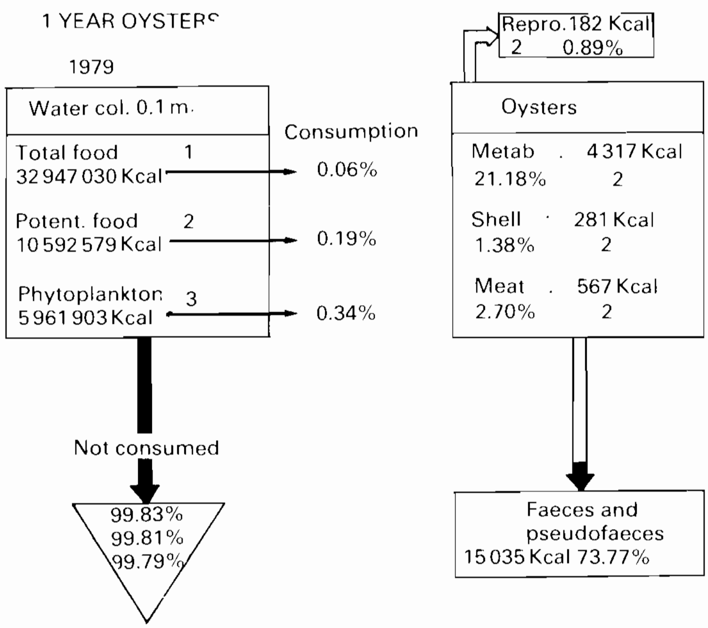


Fig. 11 — (1) Annual energy flux (1979) between the water column (0.1 m) deep in a current of 0.3 m/s and a population of two-year-old oysters reared at a density of 200 individuals/m^2 (calculated per m^2) (from Deslous-Paoli & Héral 1984). (2) Percentage of the total energy consumed calculated from levels of proteins, lipids, glucides.

factors such as the density of molluscs in the surroundings and the cumulative effect of the progressive exhaustion of the water column. No account is taken of the length of time for which the water mass remains above the areas of intensive rearing and thus the new cumulative effect linked with the time taken for wastes to be removed from the system. This time may be relatively long, particularly in semi-enclosed areas.

Elsewhere, for 1-year-old oysters, 55% of the energy is used for production of flesh, 17.75% for gamete formation, and 27.3% for the shells, while for adults, the energy is distributed as 3.6%, 78.4%, and 17.8% for the flesh, gametes and the shell. This shows that 1-year-old *C. gigas* oysters concentrate on flesh production while those in their second year direct energy towards reproductive products.

Construction of energy budgets gives information on the amount of food needed

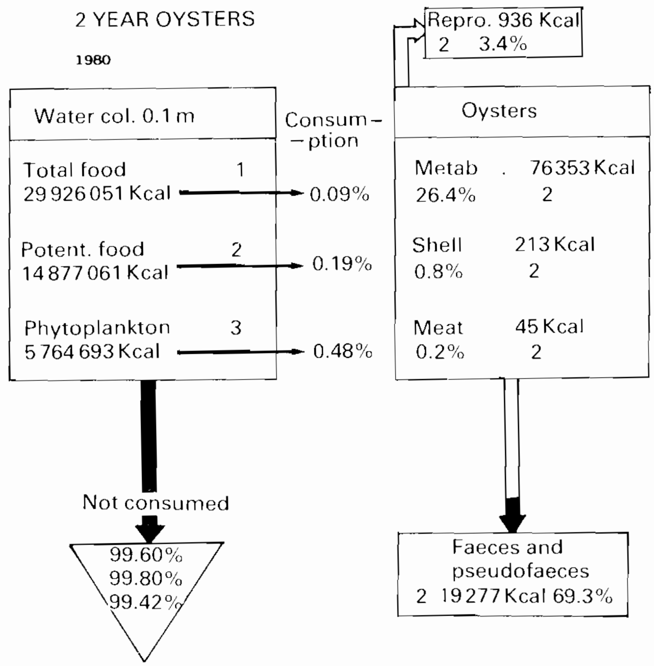


Fig. 12 — (1) Annual energy flux (1980) between a water column (0.1 m) deep in a current of 0.3 m/s and a population of two-year-old oysters reared at a density of 200 individuals/m^2 (calculated from Héral *et al.* 1983). (2) Percentage of the total energy consumed, calculated from proteins, lipids, and glucides.

by a population of oysters, and it serves as a base for the development of models of food consumption in oyster culture basins.

Similar studies are under way for the principal species which compete with the oysters for food. These include mussels, Japanese clams, cockles, and slipper limpets. Deslous-Paoli & Heral (1984) produced such a budget (Fig. 13) for the slipper limpet (*Crepidula fornicata*). They showed that 4.1 kg of slipper limpets consumed energy equivalent to that consumed by 1 kg of oysters. By studying the action of animals competing for food it should be possible to develop methods of managing and controlling their development (e.g. destruction of 2100 tonnes of slipper limpets in the Marennes–Oléron basin in 1982, 1983, and 1984).

3 STUDIES CARRIED OUT ON CULTURED STOCKS

The amount of oysters produced from culture operations can be determined from statistics available from the marine fisheries service (Fig. 1). This generally corresponds to the quantity of oysters sold with a health certificate by each producing area (basin). However, these figures give no information on the numbers of oysters in culture, which must be available to biologists designing methods of managing the oyster beds. Growth and fattening of oysters depends not only on the quantity of

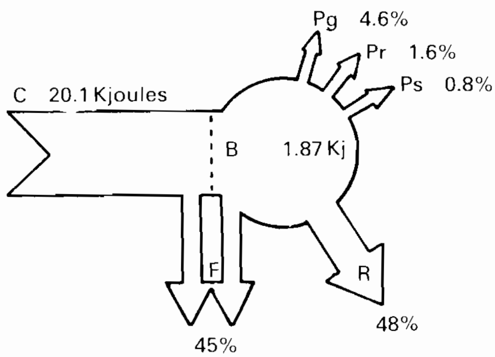


Fig. 13 — Annual energy balance for an individual of mean energy content 1.81 kJ, representative of the population of *Crepidula* in the Marennes–Oléron Basin B: biomass; C: energy used; R: energy expended in metabolism; P: energy fixed for flesh production (g), gametes (r), and the shell(s) (after Deslous-Paoli 1984).

food available but also on the abundance of competitors for food and particularly on the size of the stock in culture which fluctuates from one year to another according to the size of the spat settlement in the preceding year.

The study of stock in culture needs the implementation of a carefully designed sampling system. The most simple technique is to make a plan of the oyster beds which shows the layout of concessions, and then to take a certain number of points (2% of the area) either by random sampling, simple sampling, or stratified sampling. Two parameters must be estimated: the rate of exploitation and the biomass. Five geographical strata and two types of culture (flat and raised) were, for example, chosen for the Marennes–Oléron basin (Bacher 1984). In 1984, the amount of oysters in culture was 30 235 in flat culture with 59% of the total area exploited, and 38 594 tonnes in raised culture with 30% of the parks exploited. The error in this method of sampling is around 25%. To improve the method of estimation, aerial photography on the scale 1:10 000 allows the drawing of an improved plan, excluding unexploited areas. Aerial photographs can be used to count small culture areas and the number of culture units, and used together with actual sampling to obtain figures for biomass. On the west Contentin coast, the stock of oysters in culture in 1983 was 18 000 tonnes (Deschamps, in press), and in the Bay of Bourgneuf, in 1982, 36 400 tonnes (St Felix *et al.* 1982) with an error of 3%. For the largest areas it is possible, either by counting only randomly chosen stocks or by systematic sampling, using a 3 mm grid, to estimate exploited areas to an accuracy of 3% (Bacher 1984, Bacher *et al.* 1986). These estimates of the stocks of oysters in cultivation have been made annually since 1985 in the Marennes–Oléron Basin, in Arcachon, and in the Bay of Bourgeneuf. Accuracy of estimation is to within 6% through stratifying into types of culture and breaking down into age classes, which reduces the variance.

Actual measurements with computer-assisted analysis allows rapid treatment with optimum precision, using the image obtained from a high-resolution video. At the same time, attempts to use satellite remote sensing (simulation of SPOT) have shown that the obtainable resolution (20 μm) allows only the outlines of the cultivated areas to be determined. The absence of any unique spectral character for the oyster culture areas and the interference caused by algae which covers part of the rearing structure complicate the use of this method.

In the Mediterranean, estimation of stock size has been carried out in the étang de Thau (Hamon & Tournier 1981) by boat. The number of ropes per table is counted in each rearing zone, and then 3–4% of the cultivated area is sampled at random by divers for different depths (5 m, 5–7 m, deeper than 7 m). The different types of culture and the ages are thus determined, and the biomass on each rope weighed on land. 18923 tonnes of cupped oysters and 611 tonnes of flat oysters were grown in the étang de Thau in 1984. This figure was estimated to have a possible error of 7% (Hamon pers. comm.).

The methodology at present being developed to monotor stocks in culture is allowing the development of models for the management of culture beds which take into account the growth and maturity of the stock to be made.

4 OVERALL MODEL

It is only in the medium term, when the period of acquisition of precise information on stocks and their performance in culture has been sufficient and a knowledge of the extent of variation has been gained, that a dynamic overall model can be constructed. At present, in some culture areas (Marennes–Oléron, Bay of Bourgneuf) there are obvious signs of changing yields. An approach to the understanding of this problem can be made through the reconstruction of a historical series of productions and of yields (Heral *et al.* 1985, 1986). This historical treatment has the advantage of supplying, for the present time, overall laws covering the exploitation of the ecosystem through the culture of molluscs and supplying a basis for control. The Marennes–Oléron Basin was chosen for this method as it has almost half of the production of cupped oyster.

This model is based on the hypothesis that for the given period, environmental factors have a constant mean, although there is a certain variation around this mean. The development of production of cupped oyster in the Marennes–Oléron Basin is estimated from 1885–1984 from three different sources, as shown in Fig. 14. The time series shows that the growth rate has decreased for both Portuguese and Pacific oysters at the same time as the chronic mortality rate has increased (Fig. 15). The stocks in culture have been calculated from annual production, taking into account growth and mortality (Fig. 16). These calculations give results comparable with the estimates of stock size obtained by sampling.

The establishment of a relationship between the stock and production shows that, overall, for a given biomass in culture, production tends to platform out at a maximum level of 40000 tonnes. This level corresponds to the maximum production capacity of the ecosystem which is limited by the trophic capacity of the bay (Fig. 17). Maximum production of the ecosystem can be determined by modelling the development of the production curve, using an equation similar to that used in modelling population growth. Thus the von Bertalanffy equation takes the form $P=P_{max}(1-e^{-KB})$ where P is the maximum production in the Marennes–Oléron and B is the stock under culture. For *C. angulata*, $K=0.026$ and $P_{max}=41\,873$ tonnes; for *C. gigas*, $K=0.0288$ and $P_{max}=42\,450$ tonnes. At the same time the relationship

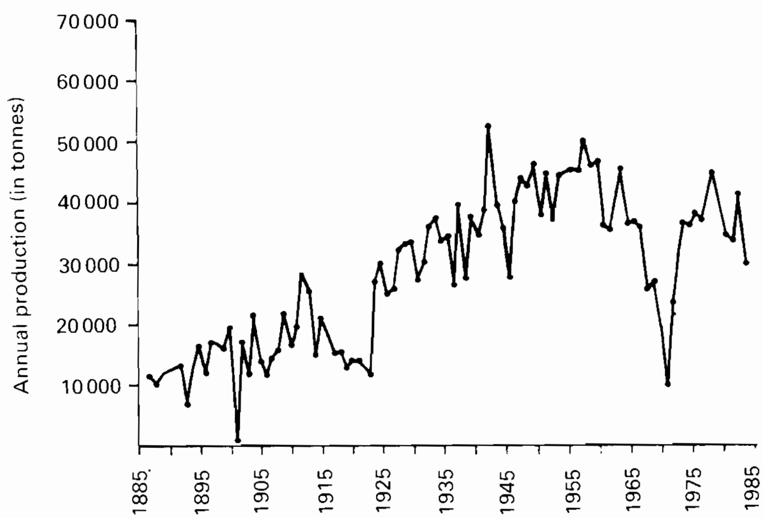


Fig. 14 — Annual production of oysters in the Marennes–Oléron Basin (after Héral *et al.* 1986).

between production and stock (*P*/*B*) as a function of the total stock in culture follows a negative exponential, leading to a decline in yields from culture.

The maximum production of 40 000 tonnes can be obtained from a stock of 130 000 tonnes of *C. angulata* and 80 000 tonnes of *C. gigas*. This difference between the two species can be ascribed to differences in the energetic requirements of each oyster. At an equal biomass, the assimilation of food by the Pacific oyster is 1.7 times greater than the Portuguese oyster (Heral *et al.* 1986). If a comparison of the effect of the two oyster species on the ecosystem is made, this conversion coefficient must be taken into account. This work demonstrates that, without management of the stock, the numbers cultivated by the oyster growers tend to exceed the minimum biomass necessary to reach the potential maximum production, and that control of the quantity of oysters in culture would bring about a decrease in the duration of the rearing cycle, in mortalities during growth, and also the probability of the occurrence of epizootics.

5 ANALYTICAL MODEL

After having shown the energy requirements of one population of oysters as well as the transfer of energy between the population and the water column and the relationship between the number of individuals in culture and production in the ecosystem, the possibility opens up of constructing a model describing the division of food and the energy requirements of the stock of molluscs to predict the growth performance of oysters in culture. The model must contain physical factors (transport) and biological factors (energetic models of growth). This approach has been used in the Marennes–Oléron Basin (Bacher 1987). The transport of food (on the

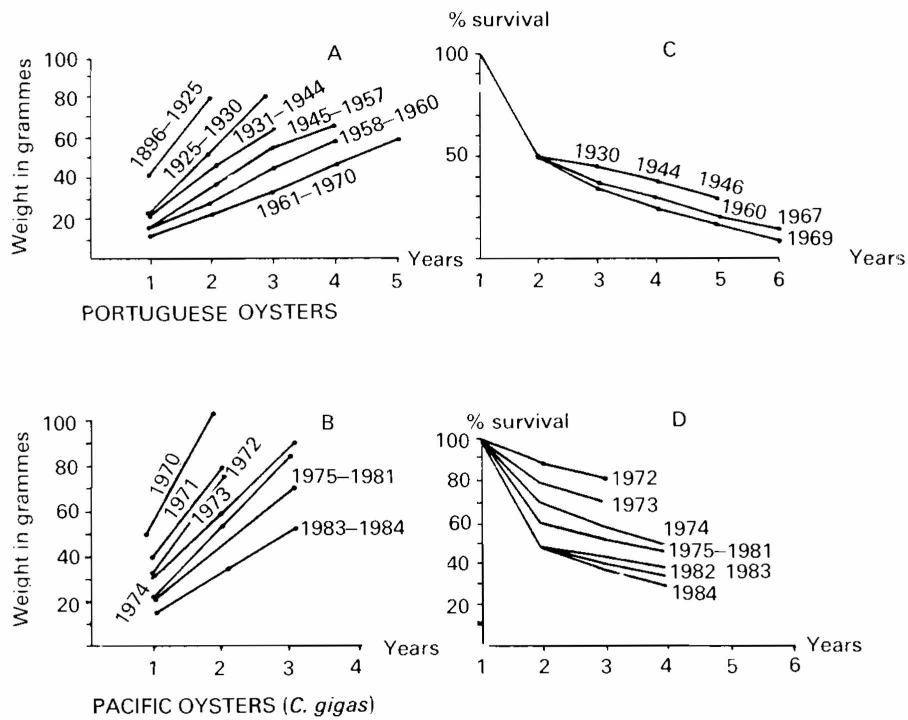


Fig. 15 — Change in growth rate needed for an oyster to reach market size. (A) Portuguese oysters, (B) Pacific oysters and survival rates after the first year of culture, (C) Portuguese oysters, (D) Pacific oysters (after Héral *et al.* 1986).

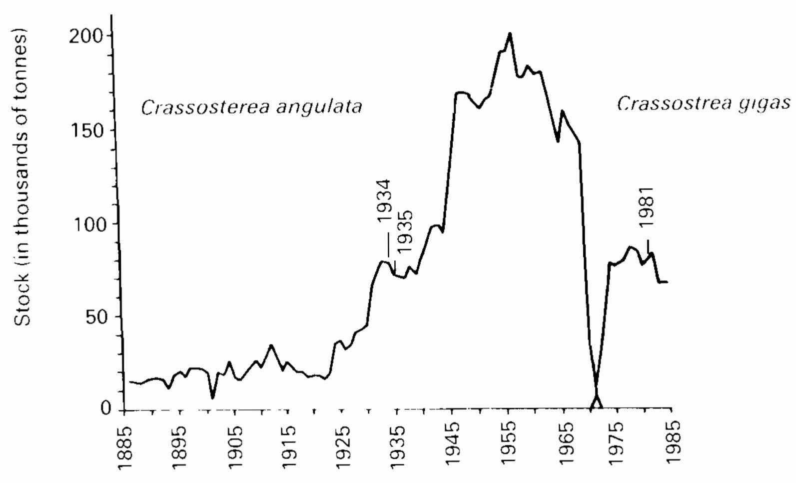


Fig. 16 — Calculated change of biomass of oysters cultured in the Marennes–Oléron Basin (After Héral *et al.* 1986).

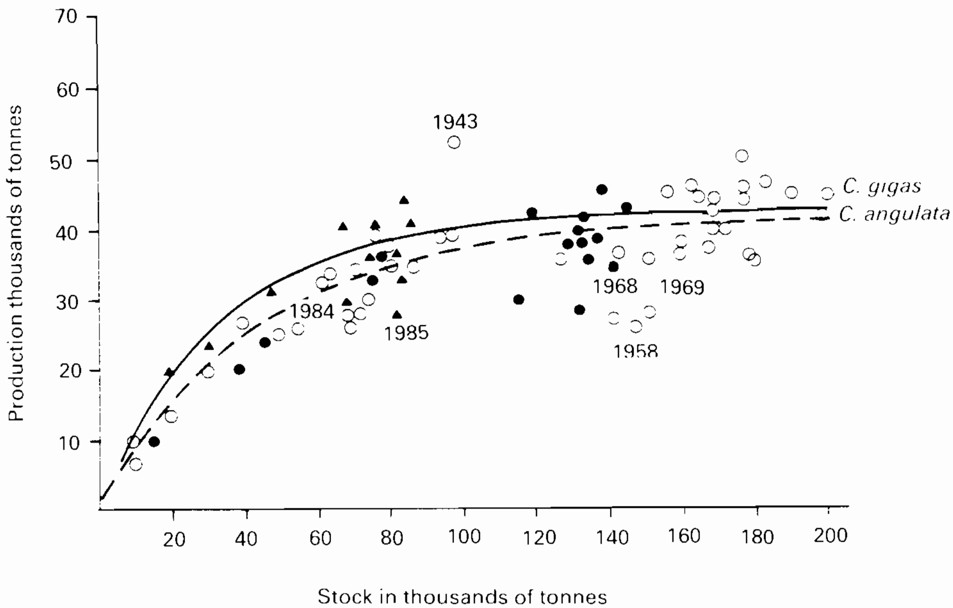


Fig. 17 — Change in production relative to biomass under culture for *Crassostrea angulata* (□), *Crassostrea gigas* (△), and *Crassostrea gigas* transformed to the equivalent *Crassostrea angulata* (*) (After Héral *et al.* 1986).

currents) was estimated by using a numerical model which gives the patterns of the currents and the depth of water. The growth of molluscs was simulated (Fig. 18), taking into account assimilation, consumption, and respiration which are related to weight, temperature, to the total available seston and the particulate energy available in the water column (Bacher 1987).

To calculate the supplies of food a compartmentalized structure is applied to the grid of the physical numerical model. The retention time is around 1 day, the Lagrangian residual currents are calculated from current tables, and dispersal is calculated by using a transport time proportional to the difference in concentrations between adjacent compartments and the tidal path estimated by using Eularian residuals at the boundary (Bacher 1987). The food supply is a forcing variable and is put into the model differently in three areas: the northern oceanic sector, the Charente estuary in the south, and in the pertuis de Maumusson.

The transport model is calculated by using a chronological series of salinities at the limits of the model. This allows the calculation of salinity at all points. Thus, in spite of a time lag in some of the salinity peaks, the amplitude of fluctuations and seasonal patterns are simulated correctly (Fig. 19).

For the calculations, the stocks of oysters in each compartment are divided into two classes, and the growth model allows growth to be simulated as a function of the food distributed in each compartment. Stock levels of competitors and their assimilation of food are introduced (Fig. 20) as a forcing variable. This approach

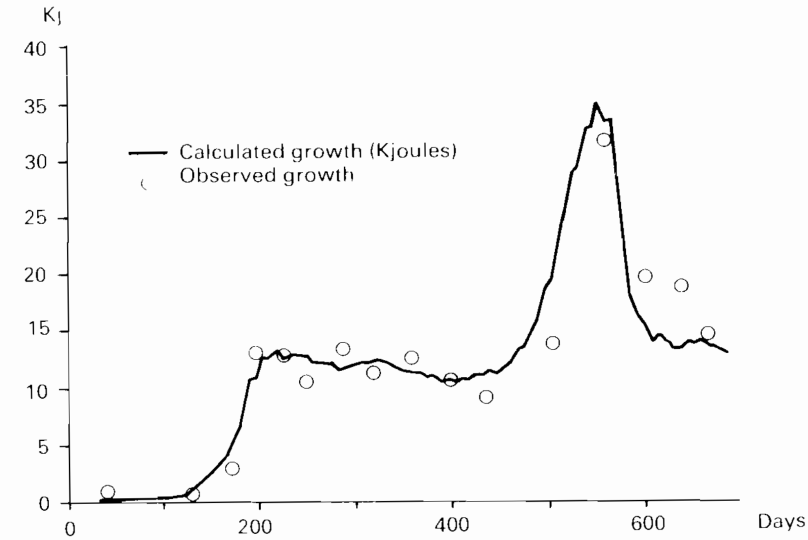


Fig. 18 — Simulation of the growth of individual oysters in kJ in relation to observed growth (after Bacher 1987).

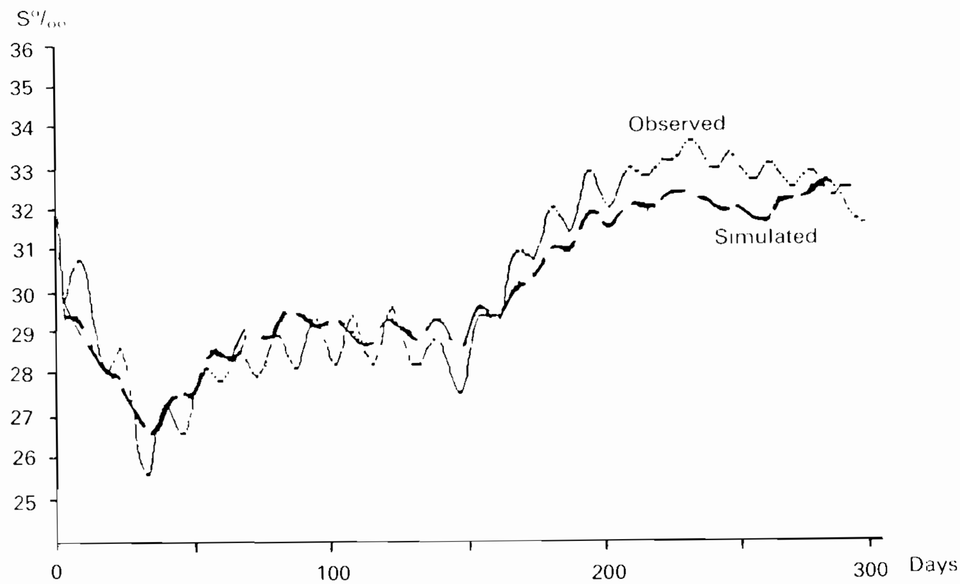


Fig. 19 — Salinities observed and calculated in a control station in the Marennes–Oléron Basis (after Bacher 1987).

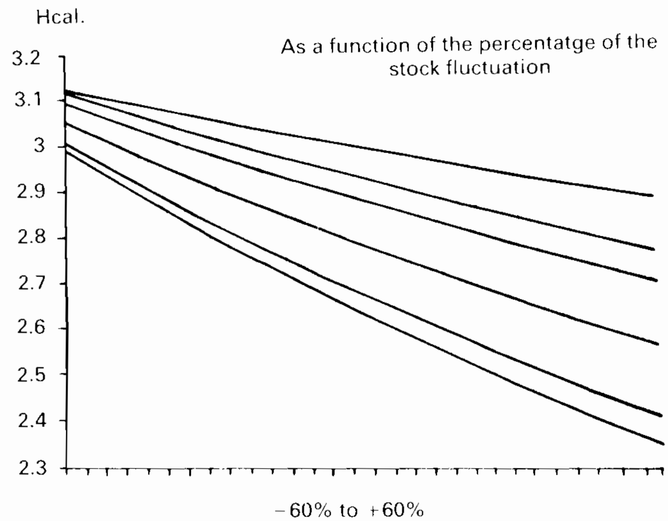


Fig. 20 — Impact of the fluctuation (−60%–+60%) of stock on individual growth for *Crassostrea gigas* (after Bacher 1987).

allows the stock levels to be varied and then predictions to be made of variations of growth in the different compartment.

This model still uses too many simplifications to be of predictive value. It could be improved by constructing:

- a predictive energetic model where the different coefficients calculated experimentally should be independent of those measured *in situ*;
- a model of the phytoplankton which allows the simulation of variations in the supplies of nutrients and which gives an indication of the impact of different methods of management of the Charente estuary.

However, this novel analytical approach, which needs a multidisciplinary approach between biologists, physicists, and sedimentologists is the only one which will allow prediction of the development of the mollusc culture ecosystems in the long term in relation to changes in densities, species cultured, food supply, run-off from the land, and man-made perturbations.

6 DISEASES

In this section, diseases which have occurred as epidemics, seriously reducing French oyster stocks since 1965, are described.

□ *Crassostrea angulata*

Marteil, (1976) described how from 1966–1969 the Portuguese oysters showed an exceptionally high mortality rate which was apparently caused by severe lesions on the gills and labial palps. This disease is referred to in France as 'maladie des branches' or gill disease. The necrosis observed was first attributed to a new species of protozoa, *Thanatastrea polymorpha,* by Franc & Arvy (1970). However, Comps & Duthoit (1976) found viral particles and lesions in the necrotic gills, the virus appearing to cause a cellular hypertrophy. Viruses have only recently been shown to affect marine invertebrates. The first description of a viral disease affecting the oyster *Crassostrea virginica* was made only in 1972. The gill disease caused a decrease in respiration (His 1969) adversely affected gametogenesis (Marteil 1969) and caused a mortality of 40% of the stock of cupped oysters from Marennes–Oléron to Arcachon.

In relation to the disease of 1970–72, Comps *et al.* (1976) presented evidence of the existence of viral particles in oysters dying in an epidemic which completely destroyed the stocks of the Portuguese oyster under culture (Plate 1). The descrip-

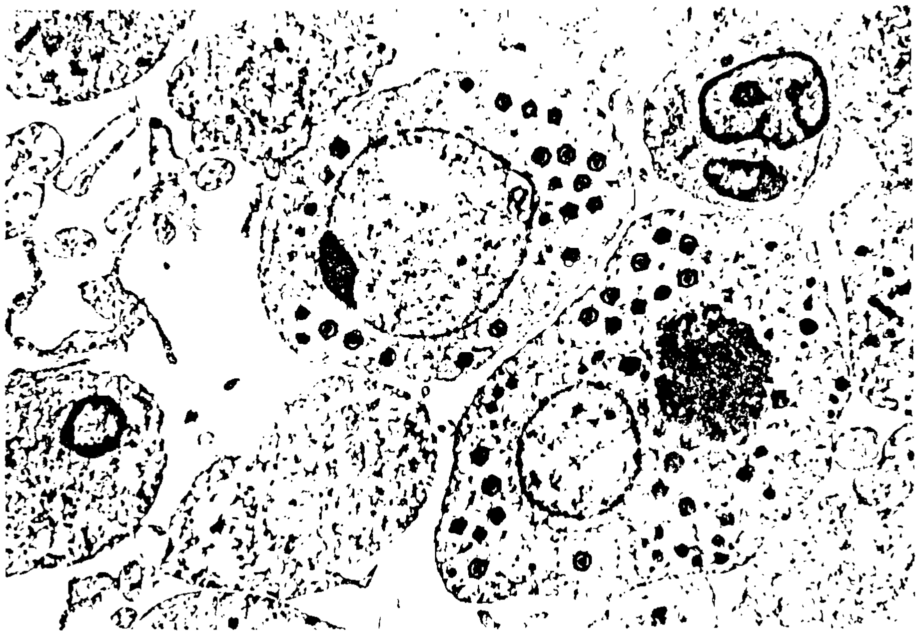


Plate 1. — Massive mortality of Portuguese oyster (1970–1973) intracytoplasmic viral lesions observed in blood cells under electronmicroscopy (×6500) (Photo M. Comps).

tion of the virus, with mature virus particle having an iso<   > structure of 350 μm, suggested that it could be classified as an *Iridovirus.* During this epidemic, around 90% of the stock of cupped oysters were killed.

□ *Crassostrea gigas*

This species, introduced into France in 1966, resisted both of the above viral attacks, demonstrating the host-specificity of the pathogens. However, during limited summer mortalities in the Arcachon Basin in 1977, viral lesions identical to those in

C. angulata in 1970 were found in *C. gigas* by Comps & Bonami (1977) which caused a reconsideration of the resistance of the Pacific oyster with respect to the *Iridovirus*. This work showed the precarious nature of the French cupped-oyster rearing-industry and encouraged growers to manage the shellfish basins better to avoid the losses consequent on periods of poor growth and physiological weakness in the oysters, which make them more susceptible to pathogenic diseases. At the same time, all imports of molluscs from other countries must be strictly forbidden to avoid the introduction of new parasites which, in certain environmental conditions, form the basis of epizootics.

The infection of *C. gigas* by *Myticola orientalis* is a recent phenomenon. This crustacean is a small, reddish-orange copepod which lives in the oyster's digestive tract. His (1977) found an infestation rate of between 10 and 40% in the Arcachon region. Up to 40 individuals develop in the intestine of the oyster where they can form a partial blockage. His *et al.* (1978) found evidence of damage to the wall of the digestive tract caused by the copepod, while Deslous-Paoli (1981) showed that in the Marennes–Oléron Basin, 64% of the cultured oysters are parasitized but 93.5% of the infected oysters have fewer than six female parasites. This appears to have little effect on the condition factor in spring and winter. However, a mean infection rate of 3 or more females gives a significant reduction in the total levels of glucides and of glycogen.

□ *Ostrea edulis*

The first mortalities began in 1968 on the north coast of Brittany and then spread rapidly to the claires of Marennes–Oléron. Little by little the parasitosis extended into almost all the centres of culture of the flat oyster, reaching the beds of south Brittany in 1975. The parasite has not yet developed in bays which are largely open to oceanic water (Quiberon, Binic, Cancale) (Grizel 1983). Comps (1970) and Herbach (1971) isolated the parasite *Martelia refringens* which is responsible for malfunction of the digestive gland.

The life cycle of the parasite and the anatomy of the different stages in its development have been studied by electron microscopy (Bonami *et al.* 1971, Grizel *et al.* 1974). The characteristics of the parasite (Fig. 21) *Martelia refringens* have led to its classification in a new protozoan genus. Its pathogenic action is probably due to a modification of cellular metabolism through the mechanical action of the closure of the digestive canal and finally through secretion of a toxin by the parasite. The disease declined after 1979, but a second disease then hit the flat oyster.

This protozoan disease was first noticed in the Ile Tudy in France, in 1979 (Comps *et al.* 1980). The parasite *Bonamia ostreae* spread rapidly through all the Breton culture centres. It induces ulcerations in the gills with perforations and indentations as well as lesions in the connective tissue. This parasite affects the older oysters particularly and causes the mortality of 50–80% of the stock. The percentage infection is lower in young oysters.

As the seed oysters show a low rate of infection with *Bonamia ostreae* and infection levels correlate with age, the plan to re-introduce the flat oyster after massive eradication of the adults entails low-density culture in deep, open water (Cancale). This technique allows the culture of several hundred tonnes of flat oysters on a three-year cycle.

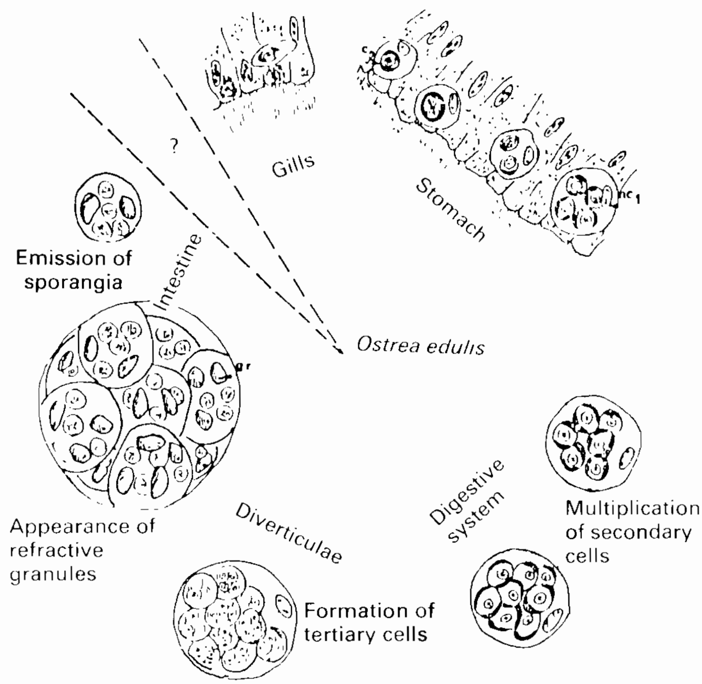


Fig. 21 — Life cycle of *Martelia refringens* for *Ostrea edulis* (after Grizel *et al.* 1974).

To improve the control of the parasites and to develop methods to prevent their spread, immunodiagnostics have been developed (Mialhe *et al.* 1987). Use of monoclonal antibodies specific for the purified parasite *Bonamia ostreae* allows rapid determination with a reliability which relates to the level of infection of the flat oysters (Fig. 22).

7 TECHNIQUES USED IN REARING

7.1 Spat production

Seed oysters for culture can be supplied in one of three ways: regulated fishing of juveniles from natural classified beds; natural capture of juveniles produced by spawners in natural stocks and in culture; and supply from a hatchery or nursery. (See Part 2 Chapter 1). The production of spat in hatcheries is of secondary importance in the French mollusc culture industry, except to make up for deficiencies in natural settlement. In this context, the development of hatcheries will go ahead only if the seed produced has benefits which make its extra cost worthwhile. If disease-resistant strains of flat oysters could be selected, or if research on the genetics of cupped oysters made triploid stocks with better growth characteristics available, the future pattern of the oyster culture industry in France would be different. The

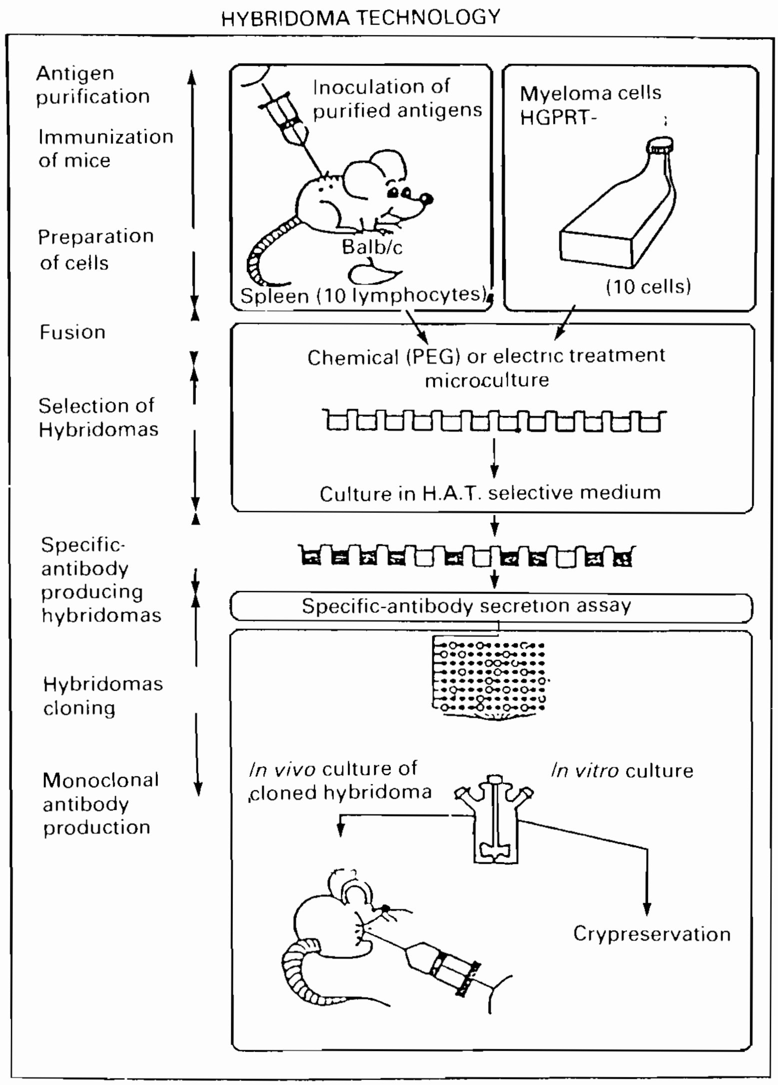


Fig. 22 — Principle of the immunodiagnostic test developed for the parasite of the flat oyster (after Mialhe *et al.* 1987).

settlement of spat on a collector provides major supply of oysters for rearing. It has already been noted that the development of oyster culture has gone hand-in-hand with the development of the technique of settlement on collectors.

☐ Types of collectors

C. gigas appears to be indifferent to the type of substrate on which it settles, which explains the great diversity of types of collectors used for spat. However, while the larvae are searching for a substrate on which to attach, fouling matter, particularly algae and silt, should be excluded. *O. edulis* is more particular in its choice of substrate for attachment.

For the cupped oyster the farmers keep to the traditional calcareous stones in the Charentes region. In the Arcachon Basin tiles coated with lime are used. These make it possible to remove the very young oysters by scraping. The tiles are arranged in cages or stacks in the parks. Stakes and wooden planks are no longer used. In all the rearing areas, on the culture tables (Fig. 23) various types of support can be used; slate posts or rods, iron bars, oyster shells, scallop shells, and slates strung out or arranged in special bags. Plastic collectors came into use at least 10 years ago; these are light, resistant, and practical from the point of view of removal of the oysters. They are either plastic tubes of various size or moulded plastic cells with oblique lamellae (Pleno).

Limed tiles are the most frequently used collector for the flat oyster. They are placed in groups at the appropriate time. The type of lime differs according to the culture region and the collector (Marteil 1979). A new type of collector consists of 'sausages' of mussel shells suspended from metal frames (Grizel *et al.* 1979) and is used in the parks in the deepest water. The mussel shells covered in spat are then separated; this removes the need for scraping.

Many studies have been carried out with the aim of determining the numbers of collectors which need to be installed as a function of the abundance of spat. Thus, in Arcachon, it has been estimated that the potential for recruitment is around 5 thousand million spat (20 million collectors with 250 spat/collector). Berthomé *et al.* (1984) measured the length of collectors by aerial photography, and, after having determined the abundance of spat on each type of collector by sampling, calculated theoretical production from settlement in 1978, 1980, and 1982 in the Seudre and Bonne Anse regions, taking into account growth and cumulative mortalities in the rearing beds. These studies clearly demonstrate the significant differences in settlement from one year to another; 1982 had a production four times greater than that in 1981. Martin *et al.* (1980) estimated the quantity of tiles positioned in the Auray region as well as using a sampling technique to estimate the settlement on each tile. They showed, from 1983 to 1986, a fall-off in the number of spat settling on each collector.

7.2 Rearing

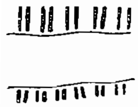
After a period varying from 6 to 18 months, according to growth and the techniques used in culture in each Basin or even sector, the seed oysters are detached from the collectors. This operation is generally carried out by hand, although mechanization is beginning to be introduced. Mortality occurring during this operation approaches 25%.

During the second year of culture the oysters may remain on the collectors which can be spaced out on the sea bed or attached to culture tables; they may be separated and placed individually on the sea bed or raised above the sea bed. They are usually reared until they are 3 years old.

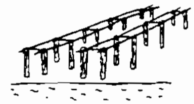
☐ Flat culture

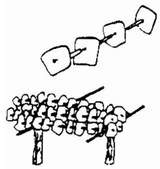
Flat culture is carried out on the uncovered sea bed. Concessions, leased to the oyster

CAPTURE INSTALLATIONS



On the left seen from above, on the right oblique view. These are made from wooden posts linked by iron bars. Their height above the sea bed varies between 0.5 m to 1 m.

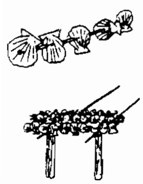




Slates threaded on a spindle arrangement

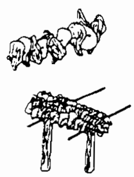
CHARACTERISTICS
Mean numberof slates per spindle = 12
Maximum number of spindles per metre of installation 50

Maximum area for spat collection = 22 m^2/m
True capture area = 15.4 m^2/m
Relative capture index = Standard collector



String of scallops/shells

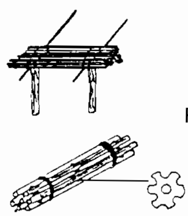
CHARACTERISTICS
Number of shells per spindle = 12
Maximum number of spindles per meter of installation = 100
Maximum area of spat collection = 30 m^2/m
True captive area = 21 m^2/m
Relative captive index = 1.05



String of oyster shells

CHARACTERISTICS
Mean number of shells per spindle – 60
Maximum number of spindles per metre installation – 90

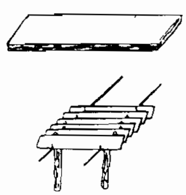
Maximum area for spat collection – 60 m^2/m
True capture area – 42 m^2/m
Relative capture index = 2.45



Plastic tube

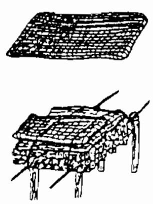
CHARACTERISTICS
Number of tubes per bundle = 7
Maximum number of bundles per metre of installation 50

Maximum capture area – 31m^2/m
True capture area – 2.7 m^2/m
Relative capture index = 1.43



Slate bars

CHARACTERISTICS
Size of bar (in cm) – 70×10×2
Number of bars per metre of installation = 20
Maximum capture area – true capture area – 3.44 m^2/m
Relative capture index not calculated



Bags of oyster shells

CHARACTERISTICS
Size of bag (in cm) – 100x50
Number of oyster shells per bag around 650
Maximum number of bags per metre installation – 10
Maximum capture area: 55 m^2/m
Remark: Never used alone but covers in a single layer other types of collectors
Relative capture index – 1.17

Fig. 23 — Different type of collector used in the Marennes–Olérin Basin (after Berthomé *et al* 1984).

growers by the state, are protected around the perimeter by plastic mesh nets so that the oysters are retained in the parks during storms. In the Gulf of Morbihan, parks for young oysters are protected from predation by crabs by mesh fences which are 30–50 cm high and are supported by wooden posts onto which horizontal planks are fixed. In the Arcachon Basin, the areas of flat culture are surrounded by hedges of twigs or stones which provide extremely effective protection. Densities of oysters vary between sectors. In the Marennes–Oléron region the mean figure is 500 kg/100 m^2 for oysters in the middle of the culture cycle, and 700 kg/100 m^2 for adult oysters (Bacher 1984). In the Arcachon region densities are of the same order of magnitude. However, according to Marteil (1979), for flat oysters it is 50–60 kg/100 m^2 in the second year, 100–120 kg/100 m^2 in the third year, and from 300 to 450 kg/m^2 in the fourth year. These densities applied before the epidemics of parasitic diseases. During their growth the oysters are regularly harrowed or forked over to avoid the beds becoming silted up.

☐ Rearing on the sea bed in deep water

This is a rearing technique which has been developed in the south of Brittany, mainly in the Bay of Quiberon, but is also used in the Bay of Cancale in northern Brittany. The densities at planting out are 50 kg/100 m^2 for seed and 70–90 kg/100 m^2 for 2-year-old oysters. Since the epizootics, a plan to safeguard the flat oyster has been implemented. The first stage was the destruction of 1367 tonnes in the parks of south Brittany and in Cancale in north Brittany. This plan was based on results from experiments which showed that densities 5 times lower than previously (100 kg/100 m^2) allowed growth over 2 to 3 years and avoided the parasitic outbreaks. All maintenance operations are carried out by dredging.

☐ Raised culture

The oysters are either still attached to the collector or enclosed in baskets which were originally made from wood but are now usually made from plastic. The most frequently used method uses net bags whose mesh increases with the size of the oysters. The standard bags which measure 1 m × 0.5 m are arranged in a line on metal tables which are 50 cm high and 4 m in length. The bags are turned over regularly to prevent the development of algae, and the numbers in the bags are halved when the biomass becomes excessive. The biomass allowed in each bag is very variable, from 5 to 15 kg depending on the age of the oyster; the mean varies from 9 to 11 kg. There are several advantages to this form of culture: better growth and quality, ease of maintenance, and low mortality from storm damage. However, there are some disadvantages: the danger of putting too many oysters in the culture system which causes poor growth and silting up (Sornin 1981) and the growth of fouling organisms on the installations which may prevent the use of this type of apparatus at certain times of year. These disadvantages have led professional operators and administrators to regulate this method of culture very strictly. For example, in the Marennes–Oléron only $\frac{1}{3}$ of the area of the concession may be cultivated in this way, and the tables must be removed in the winter to improve the transport of silt. They are installed again when the settlement of mussel spat is over.

☐ Suspended culture

This technique is used in the Mediterranean, particularly in the étang de Thau where fixed tables are constructed from old railway lines measuring 50 m in length and 10–12 m across. Each one has 51 wooden bars to which around 1000 supports can be attached (Hamon & Tournier 1981). The *C. gigas* collectors which are brought from the Atlantic are strung on lines and can be put directly onto the culture tables. Part of the stock is sold after 18 months in culture; the remainder is attached singly, with cement, by the 'heel' onto rods made from foreign hardwood. After this second year of culture, the oyster is of superior quality (Raimbault 1984). The advantage of this culture method is that the entire water column is available to the molluscs. However, the constant immersion in water leads to the development of competitors (Ascidians) and seaweed (Sargassum) on the rearing structures.

In Corsica (étang de Diane and d'Urbino) rafts are formed by floats made in the same way as the structure used in the rearing of mussels in Galicia. Oysters and mussels are reared together in suspended culture.

Recently, on the coast of Brittany and around the Golfe du Lion, cultures using suspended ropes have given promising results. (See Part 2, Chapter 54.)

7.3 The use of 'claires' to 'finish' oysters

The use of 'claires' was developed in the ancient salt marshes. They now cover an area of 3500 ha in the Marennes–Oléron Basin (Grelon 1978) and are also found on the Ile de Ré, the Bay of Bourgneuf, and in the Ile de Noirmoutier. These ponds are used for 'greening' and fattening the oysters which are stocked at a density of 25–30/m^2 for 'fines de claires' and from 4–5/m^2 for special oysters (huitres speciales). The fines de claires remain in these ponds for several weeks while the huitres speciales remain there for several months. These ponds have a high biomass of phytoplankton (Rindé 1979), particularly of a diatom *Navicula ostrearia* which is responsible for the greening of the oysters. The oysters absorb the green pigment liberated by the breakdown of the diatoms through their gills. Many studies have been carried out on the biology of this diatom in culture (Neuville & Daste 1970), while Moreau (1970) and Robert (1983) have examined the ecosystem of the claires, particularly in relation to *Navicula ostrearia*. Robert (1983) showed that nitrogen was the major limiting factor in the production of unicellular algae, and the *Navicula ostrearia* is a species which, to develop, uses oreganic matter excreted by the oysters. The research carried out on the development of the greening and the factors which control the development of *Navicula ostrearia* have been aimed at making the process less uncertain in the oyster claires of the Atlantic marshes.

8 ECONOMIC ASPECTS AND PERSPECTIVES

The production of cupped oysters oscillates around 100 000 tonnes (130 000 tonnes in 1986), which puts French oyster culture in 4th place in worldwide terms, behind the USA, Japan, and Korea. In 1982, France produced 12% of the worldwide production (FAO, 1980).

The financial return from oysters is the highest of any species under the French maritime fisheries control, reaching 1.1 thousand million francs in 1984 or 20% of the total for marine fish and shellfish, 98% of the turnover comes from cupped oysters (Fig. 24).

Activities connected with the culture of oysters occupy a large part of the littoral

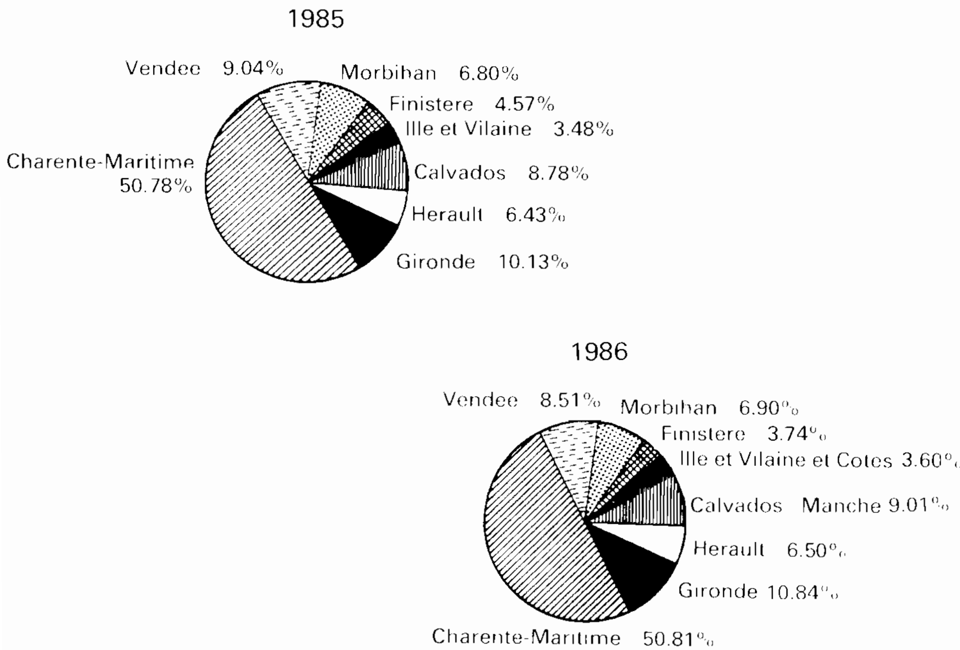


Fig. 24 — Distribution of cupped oysters sold with health tickets in the principal French producer departments in 1985 and 1986.

zone. There are 20 000 ha of concessions: 14 000 in estuaries and 6000 in deeper waters.

According to Bonnet *et al.* (1983) the oyster culture industry employs 23 000 full-time staff and 31 000 seasonally. No estimate was made of land-based jobs, but these represent a far from negligible contribution to employment: there are plastics factories making equipment for culture and packaging, boat builders, manufacturers of specific tools (graders, calibrators, etc.). The market for oysters is largely internal; there are few imports and exports. This implies that production is almost entirely dependent on the national market. According to the SECODIP panel (1983), direct sales represent 20% on average. Dumont (1983) found that between 1978 and 1982 there had been an increase from 7.9 to 17.8% in the proportion of the oysters going through the hypermarkets and supermarkets. 50% of sales take place in December, which requires well-organized marketing. The price received by the farmer is determined by syndicates in relation to the quantity and quality available. However, individual markets find their own level by mutual agreement, and prices fluctuate in relation to the product offered by the producer and the demand from the market.

The mechanism for fixing the price is far from straightforward (Fig. 25). It depends on the quantity of oysters available both locally and nationally; there is a great deal of trade between the different culture basins. The market for the cupped oyster has had to absorb an increase in production caused by improvements in techniques (raised culture) and the development of new areas (Normandy), chang-

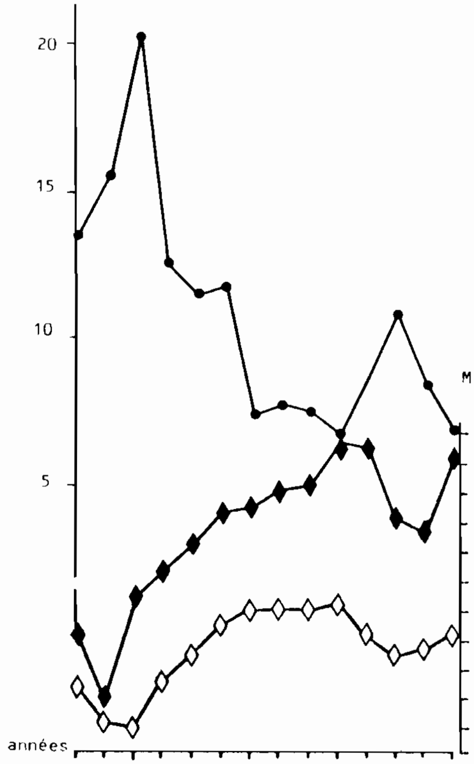


Fig. 25 — Change in the price of farmed oysters in francs (1985 prices) (●), in relation to national production (◆) and production in the Marennes–Oléron Basin (◇).

ing over from the production of flat oysters. 90% of the increase in the production of cupped oysters comes from the new regions, while the ancient basins of Marennes–Oléron and Arcachon, for example, have seen no increase in production and even a decline, linked to the biotic capacity of these over-exploited areas. Production techniques and equipment differ from one region to the next; this gives rise to differences in the sale price. Small family businesses in the old growing areas which have been divided up into small parcels have high operating costs in comparison with those in the new 'industrial' oyster culture in the developing areas.

With this competition between regions and the increase in the production of *C. gigas*, the problem of overproduction must be addressed, particularly as the price of oysters is increasing at a rate below the rate of inflation, reducing returns and causing dumping when the sale price is lower than the rearing costs. Dumont (1983) demonstrated the elasticity of the demand for cupped oysters in relation to price and income, and concluded that the difficulties faced by the oyster farmer in years of high production result from a surplus of production in relation to the marketing and distribution mechanisms. According to this author, the term 'overproduction', a surplus of production in relation to demand at a price acceptable to producers, cannot strictly be applied to cupped oysters. The problem is to determine the cost price of each oyster in the different rearing procedures and to assess whether the sale price is acceptable to the farmer. The future of the small family units in the old rearing centres will depend on reaching a relationship between rearing costs and sale price.

Two studies on the economic effects of disease in the flat oysters in Brittany have been carried out recently (Grizel 1983, Meuriot & Grizel in press). These authors have shown that the two epizootics have caused modifications to be made to the culture practice: developments toward the sea, where parasites have less effect, collection of flat oyster spat from deeper water, and an increase in the culture of *C. gigas* since 1974 with production increasing from 3000 to 16000 tonnes. In economic terms, the accumulated losses are high: 1.6 thousand million francs in turnover and 1.3 thousand million francs in added value. Comparing this with estimates of the economic consequences of the wreck of the *Amoco-Cadiz* (Bonnieus *et al.* 1980) where losses were estimated to be 114 million francs to the mollusc culture industry, it can be seen that the losses are not of the same order of magnitude. However, more care has been taken to prevent further groundings of tankers than to avoid further epizootics.

While the first disease (*Bonamia*) had only a slight effect on the numbers employed it caused the changeover to the rearing of cupped oysters. As the culture of the cupped oyster is less lucrative than that of the flat oyster, growers experienced a mean reduction in revenue, and the second epizootic in 1980 appeared to have a more direct effect on emplyment (drop of 20% in salaries between 1980 and 1982).

As has been seen from the biology, to put forward models for the management of the mollusc culture basins, which define optimum densities, it is necessary to know what stocks are being cultured. At the same time the economic approach can give reliable statistics on production and on the revenue to producers. All the politics of buying and selling should be based on a better understanding of the level of national production because the increase in the size of all the culture centres for cupped oysters increases the complexity of the market. Accurate statistics are also important for use in defending aquaculture in the competition for management of the space around the coasts.

The future development of oyster culture must take into account:

- spat settlement and the maintenance of environmental quality to give good larval survival and also the regulation of settlement with the eventual determination of a quota of collectors in order to avoid the production of surplus juveniles in relation to the food supply in the culture basins and in relation to the market;
- the distribution of cultured oysters within the basins. For good growth and fattening it is essential that the oysters should be in equilibrium with the biotic capacity of the basin;
- outbreaks of parasitic disease and, particularly, the conditions for their appearance, should be controlled by strict prohibition of the import of all molluscs and also by ensuring that the cultured stock is kept in conditions under which it can defend itself against disease. Basins must not be overstocked;
- genetic research on new stocks of oysters, aimed at directing energy ingested by *C. gigas* to the production of flesh rather than to gametogenesis. Juveniles from these new improved strains are already being produced in hatcheries;
- the development of more diverse culture. Monoculture techniques are more prone to epizootics than culture of complementary species in the ecosystem;

- marketing, particularly a study of the financial returns to each type of rearing system, allows the development of several standards of financial profitability for the development of the cupped oyster in France.

REFERENCES

Historical introduction

Coste, M. (1861) Voyage d'exploration sur le littoral de la France et de l'Italie. Paris, Imp. Impériale.

Grelon, M. (1978) Saintonge, pays des huîtres vertes. La Rochelle, Ed. Rupella, 364 p.

Hinard, G. (1927) Le contrôle sanitaire des établissements coquilliers pendant l'année 1927. *Rev. Trav. Off. Pêches Maritimes* **1** 1, 89–97

Hinard, G. & Lambert, L. (1927) Tableau de l'ostréiculture française (première partie). *Rev. Trav. Off. Pêches Maritimes* **1** 3, 37–89.

Hinard, G. & Lambert, L. (1928) Tableau de l'ostréiculture française (deuxième partie). *Rev. Trav. Off. Pêches Maritimes* **1** 4, 61–127.

Lemonnier, P. (1980) Les salines de l'Ouest, logique technique, logique sociale. Presse universitaire de Lille, Ed. Maison des sciences de l'Homme, 222 p.

Papy, L. (1941) La côte atlantique de la Loire à la Gironde. Tome 1: Les aspects naturels. Introduction à une étude de géographie humaine. Tome 2: L'homme et la mer. Etude de géographie humaine. Bordeaux, Ed. Delmas, 302 p. et 528 p.

Pizetta, J. & De Bon, M. (1880) La pisciculture fluviale en France, l'ostréiculture en France. Paris, Ed. J. Rothchild.

Roche, G. (1897) La culture des mers. Tours, Ed. Bibliothèque scientifique Internationale, 162–312.

Archives de la revue Ostréiculture, cultures marines, de 1932 à 1947.

Archives de la revue Cultures marines, de 1947 à 1983.

Statistiques des pêches maritimes. Marine Marchande, de 1867 à 1981.

Classification and geographical breakdown

Buroker, N. E., Hershberger, W. K. & Chew, K. K. (1979) Population genetics of the Family ostreidae. I: Intraspecific Studies of *Crassostrea gigas* and *Saccostrea commercialis*; II: Interspecific Studies of the genera Crassostrea and Saccostrea. *Mar. Biol.* **54** 157–169, and 54: 171–184.

Grasse, P. (1960) Traité de zoologie. Mollusques Lamellibranches, Tome V (2). Paris, Ed. Masson et Cie.

Marteil, L. (1976) La conchyliculture française, 2ème partie. Biologie d l'huître et de la moule. *Rev. Trav. Inst. Pêches Marit.*, **40** (2), 149–346.

Menzel, R. N. (1974) Portuguese and Japanese oysters are the same species. *J. Fish. Res. Bd. Canada,* **31** (4), 453–456.

Ranson, G. (1951) Les huîtres, biologie, culture. Savoir en Histoire naturelle, Vol. 23. Paris, Ed. Lechevalier, 260 p.

Ranson, G., (1967) Les espèces d'huîtres vivant actuellement dans le monde, définies par leurs coquilles larvaires ou prodissoconques. Etude des collections des grands musées d'Histoire naturelle. *Rev. Trav. Onst. Pêches marit.*, **31** (2) et (3), 128–199 et 205–274.

Physiology, absorbtion of dissolved organic matter

Amouroux, J. M. (1982) Ethologie, filtration, nutrition, bilan énergétique de *Venus Verrucosa*. Thèse de doctorat d'Etat, Université Pierre et Marie Curie, Paris VI, 1–99.

Bamford, D. R. & Gingles, R. (1974) Absorption of sugars in the gill of the Japanese oyster *Crassostrea gigas*. *Comparative biochemistry Physiology*, **49** A, 637–646.

Castell, J. D. & Trider, D. J. (1974) Preliminary feeding trials using artificial diets to study the nutritional requirements of oysters (*Crassostrea virginica*). *Journal Fisheries Research Board of Canada*, **21** 1, 95–99.

Collier, Ray, Magnitzky, O., & Bell (1953) Effect of dissolved organic substances on oysters. *Fishery Bulletin*, **84** 54, 167–183.

Ehrhardt, M. & Heinemann, J. (1975) Hydrocarbons in blue mussels from the Kiel Bight. *Environmental Pollution*, **3** 257–271.

Elliott, A. J. (1979) Laboratory investigations into the absorption of dissolved free amino acids by the gill of the mussel *Mytilus edulis* L. *Irish Fisheries Investigation*, B, **22** 1–15.

Fankboner, P. V. & De Burgh, M. E. (1978) Comparative rates of dissolved organic carbon accumulation by juvenile and pediveligers of the Japanese oyster *Crassostrea gigas* Thunberg. *Aquaculture*, **13** 205–212.

Fevrier, A. (1976) Evolution des matières organiques en solution dans l'eau de mer: relations avec l'activité métabolique des organismes marins. Thèse 3ème cycle, Université Pierre et Marie Curie, Paris VI, 1–52.

Heral, M. (1977) Etudes préliminaires des potentialités nutritives dans le bassin de Marennes–Oléron. *Océanexpo* Bordeaux, 14 p.

Heral, M., Deslous-Paoli, J. M., Razet, D., & Prou, J. (1984) Essais de mise en évidence in situ de paramètres biotiques et abiotiques de l'eau et de l'interface eau-sédiment intervenant dans la production de l'huître *C. gigas*. *Océanis*, **10**, 4, 465–475.

Jorgensen, C. B. (1982) Uptake of dissolved amino acids from natural sea water in the mussel *Mytilus edulis*, *Ophelia*, **21**, 2, 215–221.

Jorgensen, C. B. (1983) Patterns of uptake of dissolved amino acids in mussels (*Mytilus edulis*). *Mar. Biol.*, **73** 177–182.

Lucas, A. (1976) La culture des mollusques ou conchyliculture. L'exploitation de la vie marine, Océanographie biologique appliquée. Paris, Ed. Masson, 229–258.

Pequinat (1973) A kinetic and autoradiographic study of the direct assimilation of Amino acids and glucose by organs of the mussels *Mytilus edulis*. *Mar. Biol.*, **19** 227–244.

Sorokin & Wyshkwarzev (1973) Feeding on dissolved organic matter by some marine animals. *Aquaculture*, **2** 141–142.

Wright, S. M. & Stephens, G. C. (1978) Removal of amino acid during a single passage of water across the gill of marine mussels. *The journal of Expérimental Zoology*, 205 (3), 337–352.

Ingestion of particles in suspension

Fiala-Medioni, A. & Copello, M. (1984) Relations trophiques entre huître et milieu:

influence de la concentration et de la taille des particules. Colloque sur les bases biologiques de l'aquaculture. *Actes et colloques* CNEXO (sous presse), 16 p.

Gerdes, D. (1983) The pacific oyster *Crassostrea gigas*. Partie II: Oxygen consumption of larvae and adults. *Aquaculture*, **31** 221–231.

Rodhouse, P. G. (1978) The energy transformation by the oyster *Ostrea edulis* L. in a temperate estuary. *J. Exp. Mar. Ecol.*, **34** 1–22.

Widdows, J., Fieth, P. & Worrall, C. M. (1979) Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.*, **50** 195–207.

Wilson, J. M. & La Touche, R. W. (1978) Intracellular digestion in two sublittoral populations of *Ostrea edulis*. *Mar. Biol.*, **47** 71–77.

Reproduction

Deslous-Paoli, J. M., Heral, M., Berthome, J. P., Razet, D., & Garnier, J. (1981) (1982). Reproduction naturelle de *Crassostrea gigas* Thunberg dans le bassin de Marennes–Oléron en 1979 et 1981: aspects biochemiques et énergétiques. *Rev. Trav. Inst. Pêches Marit.*, **45** (4), 319–327.

Helm, M. N., Holland, D. L. & Stephenson, R. R. (1973) The effect of supplementary algal feeding of a hatchery breeding stock of *Ostrea edulis* on larval vigour. *J. Mar. Biol. Ass. U.K.* **53** 673–684.

Helm, M. N. & Millican, P. F. (1977) Experiments in the hatchery of Pacific oyster larvae (*Crassostrea gigas* Thunberg). *Aquaculture* **11** 1–12.

His, E. & Robert, R. (1980) Action d'un sel organo-métallique, l'acétate de tributyl-étain sur les oeufs et les larves D de *Crassostrea gigas* (Thunberg). *Note au C.I.E.M.*, C.M. 1980, F. 27 p.

His, E. & Robert, R. (1981) Les causes de nortalité larvaire de *Crassostrea gigas* dans le bassin d'Arcachon. *Rapport I.S.T.P.M.*, 7 septembre 1981, 31 p. + annexes.

His, E., Maurier, D., and Robert, R. (1983) Estimation de la teneur en acétate de tributyl-étain dans l'eau de mer, par une méthode biologique. Proc. 2nd. Franco-British Symp., London, 6–9 septembre 1982. *J. Moll. Stud.* Suppt. 12A, 60–68.

Lubet, P. E. (1980) Influence des facteurs externes sur la reproduction des lamellibranches. *Océnanis*, **6** (5), 469–489.

Lucas, A. (1982) La nutrition des larves de bivalves. *Océanis*, **8** (5), 363–388.

Mann, R. (1979) Some biochemical and physiological aspects of growth and gametogenesis in *Crassostrea gigas* and *Ostrea edulis* at sustained elevated temperature. *J. Mar. Biol. Ass. U.K.* **59** 95–110.

Marteil, (1976) La conchyliculture française. 2ème partie : Biologie de l'huître et de la moule. *Rev. Trav. Inst. Pêches Marit.*, **40** (2), 149–346.

Martin, Y. P. & Mengus, B. M. (1977) Utilisation de souches bactériennes sélectionnées dans l'alimentation des larves de *Mytilus galloprovincialis* Lmk (Mollusque bivalve) en élevages expérimentaux. *Aquaculture*, **10** 253–262.

Millican, P. F. & Helm, M. M. (1973) Preliminary observations on the culture of the larvae of Pacific oyster, *Crassostrea gigas* Thunberg. ICES, C. M. 1973/k, 33, 10 p.

Millar, R. H. & Scott, J. M. (1967) The larval of oyster *Ostrea edulis* during starvation. *J. Mar. Biol. Ass. U.K.*, **47** 475–484.

Prieur, D. (1980) Les relations entre mollusques bivalves et bactéries hétérotrophes en milieu marin. Etude analytique et expérimentale. Thèse d'état, Université de Bretagne Occidentale, 266 p.

Robert, R. (1983) Etudes sur les causes de la perturbation de la reproduction et du développement larvaire de *Crassostrea gigas* dans le bassin d'Arcachon. Thèse 3ème cycle, Université de Bretagne Occidentale, 169 p.

Robert, R. & His, E., (1981) Action de l'acétate de tributyl-étan sur les oeufs et larves D de deux mollusques d'intérêt commercial: *Crassostra gigas* (Thunberg) et *Mytilus galloprovincialis* (LmK). *Note au C.I.E.M.* C.M. 1980/E, p. 42.

Energy budget

Anonyme (1987) Bilan énergétique chez les mollusques bivalves: terminologie et méthodologie. *Vie marine*, Hors série No. 7, 68 p.

Bayne, B. L., Thompson, R. J. & Widdows, J. (1976) Physiology I. In: Bayne B. L., Ed. Marine mussels, their ecology and physiology. Cambridge University Press, I.B.P. 10, 121–206.

Bernard, F. R. (1974) Annual biodeposition and gross energy budget of mature pacific oysters. *Crassostrea gigas. J. Fish. Res. Board. Can.*, **31** (2), 185–190.

Boukabous, R., (1983) Etude préliminaire des adaptations écophysiologiques de l'huître *Crassostrea gigas* (Thunberg) dans la lagune de Oualidia. Mémoire 3ème cycle Agronomie, Institut Agronomique et Vétérinaire Hassan II (Maroc), 51p.

Copello, M. (1982) Données écophysiologiques sur un organisme filtreur benthique de étangs littoraux méditerranéens : *Crassostrea gigas.* Rapport de DEA, Université Paris VI.

Deslous-Paoli, J. M., Heral, M. & Zanette, Y. (1982) Problèmes posés par l'analyse des relations trophiques huîtres-milieu. *In* Indices biochemiques en milieuxmarins. Journées du GABIM, Bres 18–20 novembre 1981. *Publ. CNEXO (Actes de colloques)*, **14** 335–340.

Deslous-Paoli, J. M. & Heral, M. (1984) Transferts énergétiques entre l'huître *Crassostrea gigas* de 1 an et la nourriture potentielle disponible dans l'eau d'un bassin ostréicole. *Haliotis*, **14** 79–90.

Deslous-Paoli, J. M., Heral, M. & Masse, H., (1985) Bilan énergétique d'une population naturelle de *Crepidula fornitica* dans le bassin de Marennes–Oléron. Bases biologiques de l'Aquaculture, Montpellier 1983. IFREMER, *Actes de Colloques*, **1** 109, 124.

Deslous-Paoli, J. M. (1985) Assessment of energetic requirements of reared molluses and of their main competitors. In Aquaculture: Shellfish culture development and management, La Rochelle, March 1985, Edt IFREMER, 31–346.

Deslous-Paoli, J. M., Heral, M., Goulletquer, P., Boronthanarat, W., Razet, D., Garneir, J., Prou, J. & Barillet, L. (1986) Evolution saisonnière de la filtration de bivalves intertidaux dans des conditions naturelles. GABIM La Rochelle, *Océanis*, sous presse.

Deslous-Paoli, J. M., Heral, M., Goulletquer, P., Boronthanarat, M., Prou, J., Razet, D. & Garnier, J. (1987) Efficiency of particle retention and filtration rate in intertidal bivalve molluscs: seasonal variations under natural conditions. Poster EMBS Barcelona Septembre 1987.

Griffins, R. J. (1980) Natural food availability and assimilation in the bivalves *Choromytilus meridionalis. Mar. Ecol.*, **3** 151–156.

Heral, M. & Deslous-Paoli, J. M. (1983) Valeur énergétique de la chair de l'huître *Crassostrea gigas* estimée par mesures microcalorimétriques et par dosages biochimiques. *Océanol. Acta.* **6** (2), 193–199.

Heral, M., Deslous-Paoli, J. M. & Sornin, J. M., (1983) Transferts énergétiques entre l'huître *Crassostrea gigas* et la nourriture potentielle disponible dans un bassin ostréicole: premières approches. *Océanis,* **9** (3), 169–194.

Heral, M. (1985) Evaluation of the carrying capacity of molluscan shellfish ecosystems. In Aquaculture: Shellfish culture development and management. La Rochelle, March 1985 edit; IFREMER, 297–318.

Heral, M., Deslous-Paoli, J. M. & Prou, J. (1986) Influence de climat sur le recrutement et sur la production d'huîtres cultivées (*Crassostrea angulata* et *Crassostrea gigas*) dans le bassin de Marennes–Oléron (France). *Note au CIEM* comité de la Mariculture F/40, 20 p.

Heral, M., Deslous-Paoli, J. M., Goulletquer, P., Razet, D., Prou, J., Ravail, B. Vincendeau, M. L., (1987) Variations saisonnières de l'excrétion azotée et respiration de 5 mollusques intertidaux: l'huître (*Crassostrea gigas*), la moule (*Mytilus edulis*), la coque (*Cerastoderma edule*), la palourde japonaise (*Ruditapes philippinarus*) et la crépidule (*Crepidula fornicata*). Haliotis, sous presse.

Kiørboe, T., Møhlenberg, F. & Nøhr, O. (1981) Effect of suspended bottom material on growth and energetics in *Mytilus edulis. Mar. Biol.*, **61** 283–288.

Lucas, A. (1982) Remarques sur les rendements de production chez les bivalves marins. *Haliotis,* **12** 47–60.

Mac Fayden, A. (1966) Les méthodes d'étude de la productivité des invertébrés dans les écosystèmes terrestres. *La terre et la vie,* **4** 361–392.

Shafee, M. S. & Lucas, A. (1982) Variations saisonnières du bilan énergétique chez les individus d'une population de *Chlamys varia* (L.) (*Bivalvia, Pectinidae*). *Oceanol. Acta.*, **5** (3), 331–338.

Odum, E. D. (1971) Fundamentals of Ecology. Philadelphia 3rs Ed. Sounders, p. 254.

Sornin, J. M., Feuillet, M., Heral, M. & Deslous-Paoli, J. M. (1983) Effet des biodépôts de l'huître *Crassostrea gigas* (Thunberg) sur l'accumulation des matières organiques dans les parcs du bassin de Marennes–Oléron. *J. Moll. Study*. Suppt. 12A, 12 p.

Thompson, R. J. & Bayne, B. L. (1974) Some relationship between growth, metabolism and food in the mussel *Mytilus edulis. Mar. Biol.* **27** 317–326.

Vahl, D., (1981) Energy transformation by the Iceland scallop *Chlamys islandica* (D. F. Muller) from 70°N. I: The age specific energy budget and net growth efficiency. *J. Exp. Mar. Biol. Ecol.* **53** 281–296.

Walne, P. R. (1970) The seasonal variation of meat and glycogen content of seven populations of oysters *Ostrea edulis* L. and a review of the literature. *Fish. Invest.*, **2** p. 35.

Winter, J. E. (1976) Feeding experiments with *Mytilus edulis* L. at small laboratory scale. II. The influence of suspended silt in addition of algal suspensions on growth. *Proc. 10th Eur. Symp. Mar. Biol.*, Ostende, Belgique, 583–600.

Winter, J. E. (1978) A critical review on some aspects of filter-feeding lamellibranchiate bivalves. *Haliotis*, **7** 71–87.

Widdows, J. (1978) Combined effects of body size, Food in the mussel *Mitylus edulis*. *J. Mar. Biol. Ass. U.K.*, **58** 109–124.

Models

Bacher, C. (1985) Development of shellfish production models. In Aquaculture: Shellfish culture development and management, La Rochelle, March 1985, Edit. IFREMER: 347–362.

Bacher, C. (1987) Modélisation de la croissance des huîtres dans le bassin de Marennes–Oléron. Rapport IFREMER-CNRS, Octobre 1987, 12 p.

Heral, M., Deslous-Paoli, J. M. & Prou, J. (1985) Analyse historique de la production conchylicole du bassin de Marennes–Oléron (France). *Coll. Fr. Japon Oceanogr. Marseille*, 16–21 sept. 1985, **7** 55–65.

Heral, M., Deslous-Paoli, J. M. & Prou, J. (1986) Dynamique des productions et des biomasses des huîtres creuses cultivées (*Crassostrea angulata* et *Crassostrea gigas*) dans le bassin de Marennes–Oléron depuis un siècle. *Note au CIEM*, Comité de la Mariculture F/41, 22 p.

Stocks in culture

Bacher, C. (1984) Echantillonnage du stock d'huîtres du bassin de Marennes–Oléron, Rapport de DEA, Université de Paris, 38 p.

Hamon, P. Y. & Tournier, H. (1981) Estimation de la biomasse en culture dans l'étang de Thau. *Sciences et Pêches. Bull. Inst. Pêches Marit.* No. 313, 38 p.

Saint-Felix, C., Baud, J. P., & Homebon, P. (1982) Estimation de la biomasse ostréicole de la Baie de Bourgneuf. *Science et Pêche, Bull. Inst. Pêches Marit.*, 3–9.

Disease

Bonami, J. R., Grizel, H., Vago, C. & Duthoit, J. L. (1971) Recherche sur une maladie épizootique de l'huître plate *Ostrea edulis* Linné. *Rev. Trav. Inst. Pêches Marit.*, **35** (4), 415–418.

Comps, M. (1970) Observations sur les causes d'une mortalité anormale des huîtres plates dans le bassin de Marennes. *Cons. Int. Explor. Mer.*, K4, 7 p.

Comps, M., Bonami, J. R., Vago, C. & Campillo, A. (1976) Une virose de l'huître portugaise *Crassostrea angulata*. *C. R. Acad. Sci.*, Paris, 282 série D., 1991–1993.

Comps, M. & Duthoit, J. L. (1976) Infection virale associée à la "maladie des branchies" de l'huître portugaise *Crassostrea angulata*. *C. R. Acad. Sci.*, Paris, 283 série D, 1595–1597.

Comps, M., Bonami, J. R. (1977) Infection virale associée à des mortalités chez l'huître *Crassostrea gigas* Thunberg. *C. R. Acad. Sci.*, Paris, 285, série D., 1139–1140.

Comps, M., Tige, G. & Grizel, H. (1980) Etude ultrastructurale d'un protiste parasite de l'huître plate *Ostrea edulis*. *C. R. Acad. Sci.*, Paris, 290, série D, 383–385.

Deslous-Paoli, J. M. (1981) *Mytilicola orientalis* Mori, *Crassostrea gigas* Thunberg's parasite, in the bassin of Marennes–Oléron: impact on the condition and the biochemical composition of oysters during rearing. *Cons. Int. Explor. Mer.*, K 29, 16 p.

Franc, A. & Arvy, L. (1970) Données sur l'évolution de la "maladie des branchies" chez les huîtres et sur son agent causal: *Thanatostrea polymorpha* Franc et Arvy, 1969. *Bull. Biol.*, **104** (1).

Grizel, H., Comps, M., Bonami, R., Cosserans, F. & Duthoit, J. L. (1974) Recherche sur l'agent de la maladie de la glande digestive *Ostrea edulis* Linné. *Science et Pêche, Bull. Inst. Pêches Marit.*, **240** 7–30.

Grizel, H. (1983) Impact de *Marteilia refringens* et *Bonamia ostreae* sur l'ostréiculture bretonne. *Cons. Int. Explor. Mer.*, G 9, 30 p.

Herbach, B. (1971) Sur une affection parasitaire de la glande digestive de l'huître plate *Ostrea edulis* Linné. *Rev. Trav. Inst. Pêches Marit.*, **35** (2), 79–87.

His, E. (1969) Recherches d'un test permettant de comparer l'activité respiratoire des huîtres au cours de l'évolution de la maladie des branchies. *Rev. Trav. Inst. Pêches Marit.*, **33** (2), 171–175.

His, E. (1977) Observations relatives à l'infestation de *Crassostrea gigas* Thunberg par le copépode parasite *Mytilicola orientalis* Mori dans le bassin d'Arcachon. *Cons. Int. Explor. Mer.*, K 33, 10 p.

His, E., Tige, G. & Rabouin, M. A. (1978) *Mytilicola orientalis* Mori: son action sur les huîtres de bassin d'Arcachon au cours de l'été et de l'automne 1977. *Cons. Int. Explor. Mer.*, K 14, 12 p.

Marteil, L. (1969) Données générales sur la maladie des branchies. *Rev. Trav. Inst. Pêches Marit.*, **33** (2), 145–150.

Mialhe, E., Paolucci, F., Rogier, H. & Grizel, H. (1987) Monoclonal antibodies: a new tool in mollusc pathology. In: Disease Process In Marine Bivalve Molluscs publié par: American Fisheries Society, Special Publication Series, (in press).

Culture techniques

Berthome, J. P., Prou, J., Razet, D. & Garnier, J. (1984) Première approche d'une méthode d'estimation prévisionnelle de la production potentielle d'huître creuse *C. gigas* d'élevage. *Haliotis*, **14** 39–48.

Grizel, H., Langlade, A. & Perodu, J. B. (1979) Premiers essais d'une nouvelle technique de captage d'huître plate en Baie de Quiberon. *Cons. Int. Explor. Mer.*, K 24, 14 p.

Marteil, L. (1979) La conchyliculture française, 3ème partie. *Rev. Trav. Inst. Pêches Marit.*, **43** (1), 5–130.

Martin, A. G., Grizel, H. & Langlade, A. (1980) Evaluation du recrutement d'huîtres plates (*Ostrea edulis*) collectées sur tuile dans le quartier d'Auray (Bretagne) en 1979. *Cons. Int. Explor. Mer.*, K 31.

Moreau, J. (1970) Contribution aux recherches écologiques sur les claires à huîtres du bassin de Marennes–Oléron. *Rev. Trav. Inst. Pêches Marit.*, **34** 380–462.

Neuville, D. & Daste, Ph. (1970) Premières observations concernant la culture unialgale de souches de Diatomées provenant de claires ostréicoles de l'Ile d'Oléron. *C.R. Acad. Sci.*, Paris, **270** série D, 2486–2488.

Neuville, D. (1978) Les diatomées des claires ostréicoles. Contribution des techniques de culture in vitro à l'étude de leur biologie. Thèse Doct. Etat, Univ. Poitiers, 279 p.

Raimbault, R. (1984) La conchyliculture en Méditerranée Française. *Haliotis*, **14** 1–22.

Rince, Y. (1979) Cycle saisonnier des peuplements phytoplanctoniques et microphytobenthiques des claires ostréicoles de la baie de Bourgneuf. *Rev. Algal.*, **14** 297–313.

Robert, J. M., Maestrini, S. Y., Heral, M. & Zanette, Y. (1982) Production des micro-algues des claires ostréicoles en relation avec l'azote organique dissous, excrété par les huîtres. Silco, Bordeaux, septembre 81. *Oceanol. Acta.* no sp., 389–395.

Robert, J. M. (1983) Fertilité des eaux des claires ostréicoles et verdissement. Utilisation de l'azote par les diatomées dominantes. Thèse doct. Etat, Université de Nantes, 281 p.

Sornin, J. M. (1981) Processus sédimentaires et biodéposition liés à différents modes de conchyliculture. Thèse 3ème cycle, 188 p.

Economics

Bonnet, M., Dardignac-Corbeil, M. J. & Duclerc, J. (1983) L'aquaculture marine française, bilan et perspectives. Note A.P.P., 17 p.

Bonnieux, F., Dauce, P. & Rainelli, P. (1980) Impact socio-économique de la marée noire provenant de l'Amoco-Cadiz. Rapport INRA-UVLOE, 100 p.

Dumont, P. (1983) Le marché de l'huître creuse. Essai de modélisation économique. Rapport ENGREF, 58 p + annexes.

Meuriot, E. & Grizel, H. Note sur l'impact économique des maladies de l'huître plate en Bretagne (in press).